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TABLE OF CONTENTS.

PAGE

On the origin and nature of the middle lamella - - - *Charles E. Allen* 1

Structural studies on southwestern Cactaceae (with nine figures) - - - - - - - - - - *Carleton E. Preston* 35

Gametogenesis and fertilization in Albugo. Contributions from the Hull Botanical Laboratory. XXIX (with plates I–IV) - - - - - *Frank L. Stevens* 77, 157, 238

The ecological relations of the vegetation of western Texas. Contributions from the Hull Botanical Laboratory. XXX (with twenty-four text figures) - - *William L. Bray*, 99, 195, 262

A study of the sporangia and gametophytes of Selaginella apus and Selaginella rupestris. Contributions from the Hull Botanical Botanical Laboratory. XXXI (with plates V–IX) - - - - - - - *Florence M. Lyon* 124, 170

The application of normal solutions to biological problems *James B. Dandeno* 229

Further notes on the physiology of polymorphism in green algae. Contributions from the Hull Botanical Laboratory. XXXII - - - - - - *Burton Edward Livingston* 292

New or little known unicellular algae. II. Eremosphaera viridis and Excentrosphaera (with plates X–XII) *George Thomas Moore* 309

Development of the pollen in some Asclepiadaceae. Contributions from the Hull Botanical Laboratory. XXXIII (with plate XIII) - - - - - - - *T. C. Frye* 325

On the distribution of red color in vegetative parts in the New England flora - - - - - - - - - - *F. Grace Smith* 332

Some plant abnormalities (with thirty-six figures) - *George Harrison Shull* 343

The anatomy of the Osmundaceae (with plates XIV–XVII) *J. H. Faull* 381

BRIEFER ARTICLES—

Note on Basilima and Schizonotus of Rafinesque - *Alfred Rehder* 56

Potamogeton polygonifolius in Newfoundland, - - *Arthur Bennett* 58

A new Sphaeralcea - - - - - - - - - - *T. D. A. Cockerell* 60

The probable function of calcium oxalate crystals in plants - - - - - - - - - - - *Albert Schneider* 142

Notes of travel. VII - - - - - - - *David G. Fairchild* 218

Intramolecular respiration - - - - - - *T. C. Johnson* 303

Notes on Aquilegia Canadensis Linn. and A. vulgaris Linn. - - - - - - - - - *J. Schneck* 304
Meissner on evergreen needles (with one figure) *Edwin Bingham Copeland* 356
The instability of the Rochester nomenclature - - *M. L. Fernald* 359
Flower visits of oligotropic bees. III - - - - *Charles Robertson* 367
Some erroneous references - - - - - - *E. W. D. Holway* 421
Puccinia inanipes - - - - - - - - - - *E. W. D. Holway* 422
The position of pleurococcus and mosses on trees - *Henry Kraemer* 422
Contribution to the knowledge of the physiology of karyokinesis (with one figure) - - - - - *Arthur Carr Lewis* 423

OPEN LETTERS—

Normal solutions - - - - - - - *Louis Kahlenberg* 437 / *James B. Dandeno* 439
Basilima, Schizonotus, Sorbaria - - - - *John Hendley Barnhart* 440

CURRENT LITERATURE— - - - - - - 61, 145, 218, 306, 369, 426

For titles see index under author's name and Reviews. Papers noticed in "Notes for Students" are indexed under author's name and subjects.

NEWS— - - - - - - - - - - - - 74, 154, 227, 307, 379, 443

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ERRATA.

P. 45, line 5 from below, for composed, read compressed.

P. 50, line 14, for "In the absorptive roots the elements are wider, more regular and less thickened," read "In the absorptive root the medullary rays are narrow and of thin-walled cells containing crystals; in the anchoring root, the elements are wider, more regular and without crystals."

P. 70, line 7 from below, for Laminaceae read Laminariaceae.

P. 71, line 15 from below, insert parenthesis before *Ceramothamnion*.

P. 76, line 13, for aaother read another.

P. 78, line 9, for *artemisaefolia* read *artemisiaefolia*.

P. 120, line 9 from below, for vegeation read vegetation.

P. 158, in legend of center figure of first row, insert one before functional.

P. 166, line 20, for Monoblepharadineae read Monoblepharidineae.

P. 212, legend of figure 12, for J. sabinioides read J. sabinoides.

P. 237, line 1, for 1899 read 1889.

P. 255, line 12, for philogenetically read phylogenetically.

P. 285, legend figure 23, for Tomillo read Tornillo.

P. 303, line 13, from below, for they read it.

P. 306, heading, for LITERATRUE read LITERATURE.

P. 325, line 4 of title, for XXXII read XXXIII.

P. 375, line 17, for byrological read bryological.

On plates I, II, and III, at head, for XXVII read XXXII.

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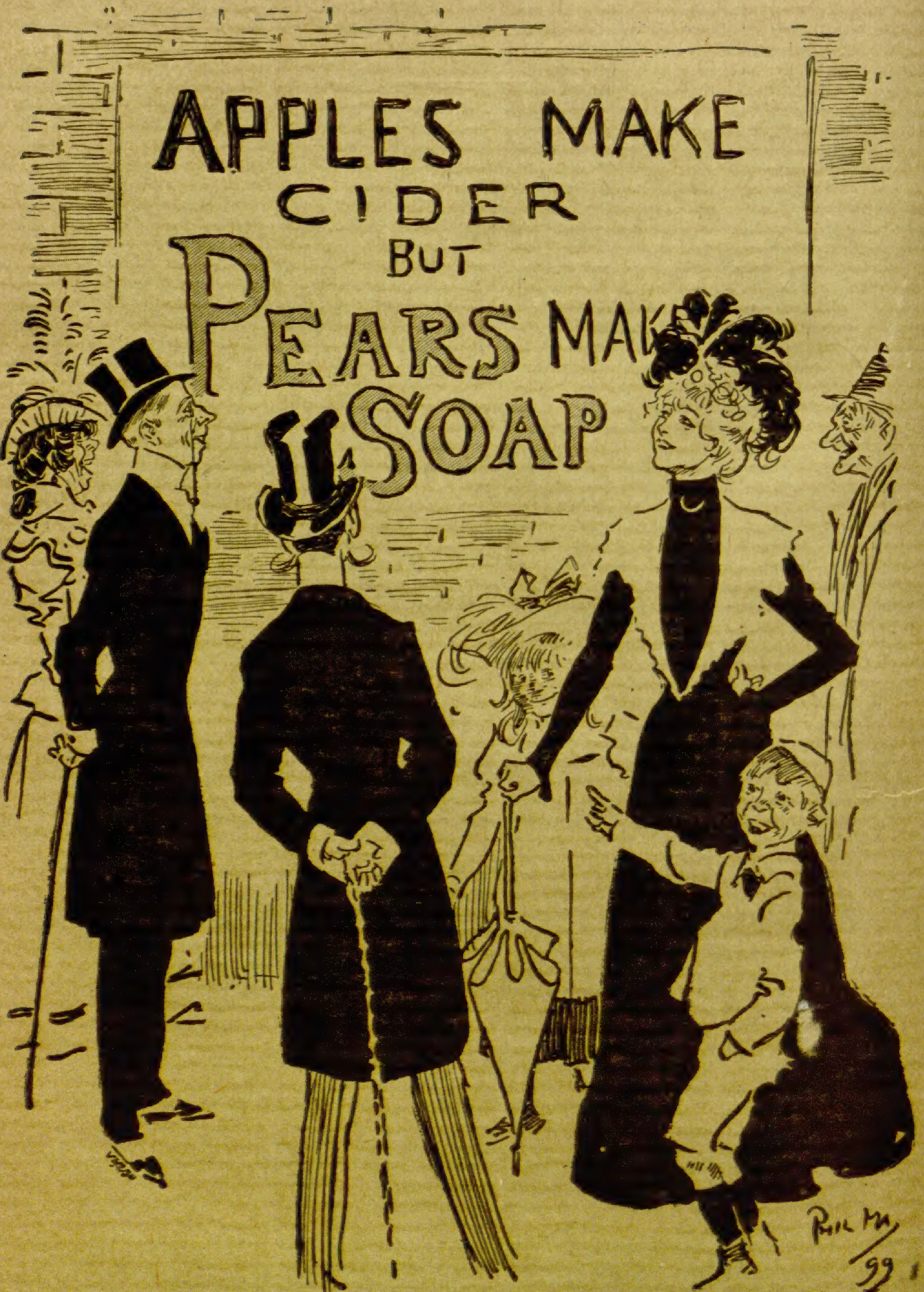

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CONTENTS

ON THE ORIGIN AND NATURE OF THE MIDDLE LAMELLA. *Charles E. Allen* 1

STRUCTURAL STUDIES ON SOUTHWESTERN CACTACEAE (WITH NINE FIGURES). *Carleton E. Preston* - - - - - - - - - - - - - - - - 35

BRIEFER ARTICLES.

NOTE ON BASILIMA AND SCHIZONOTUS OF RAFINESQUE. *Alfred Rehder* - - - 56

POTAMOGETON POLYGONIFOLIUS IN NEWFOUNDLAND. *Arthur Bennett* - - - 58

A NEW SPHAERALCEA. *T. D. A. Cockerell* - - - - - - - - - - - 60

CURRENT LITERATURE.

BOOK REVIEWS - - - - - - - - - - 61

HANDBOOK OF SYSTEMATIC BOTANY.

MINOR NOTICES - - - - - - - - - - 62

NOTES FOR STUDENTS - - - - - - - - - 63

NEWS - - - - - - - - - - - - 74

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JULY, 1901

ON THE ORIGIN AND NATURE OF THE MIDDLE LAMELLA.

CHARLES E. ALLEN.

THERE has long been recognized in the cell walls of plant tissues, and particularly in the thickened walls of bast and xylem elements in woody plants, a central layer or plate, sharply distinguishable by its optical and staining properties from other regions of the wall. To account for the origin of this layer, apparently homogeneous and equally closely related to each of the cells between which it occurs, various theories have been advanced, and the names "primary cell wall," "intercellular substance," and "middle lamella" indicate the diversity of opinion that has prevailed as to its real nature.

The theories of the origin of this "middle lamella," adopting as most convenient its commonest designation, may (1), generally speaking, be grouped under three heads: (1) those which hold it to have been originally a common matrix in which the cells were imbedded; (2) the theory that the middle lamella is the original cell wall, laid down in common by the two daughter cells in the process of cell division, and remaining distinct from the secondary thickening layers deposited upon its either face; and (3) the view that it is a substance excreted by the daughter cells into a space left between them after their formation, or into a space formed by their rounding up and drawing apart.

The first theory, that the middle lamella is an original common matrix of the cells, was shown to be groundless as soon as any satisfactory investigation of the process of cell division could be made.

The notion of the middle lamella as the primary cell wall until very recently was the most prevalent, and is the one still laid down in most text-books of botany. Vines (**15**) thus states this view:

> In the development of a tissue, whether by free cell formation or by cell division, septa are formed, that is, walls which are common to contiguous cells; these are very thin at first, and appear under the highest magnifying power as a simple plate. As the walls increase in thickness and acquire a more or less distinctly stratified structure, as seen in transverse section, the network of primary septa stands out from the thickening layers proper to each cell. The primary septum between any two cells is now distinguished as the *middle lamella* (sometimes also termed *intercellular substance*); it attains a considerable bulk at points where several septa meet at an angle.

This theory was early stated by Strasburger, and until lately he has adhered to it in unmodified form. In the first edition of the *Botanisches Practicum* (**10**), on p. 78, he describes a method of demonstrating the presence of this median layer in the endosperm of the seed of *Ornithogalum umbellatum* by treatment with sulfuric acid, the delicate network of the middle lamella being the last part of the cell walls to dissolve. This network, he says, corresponds to the original walls present before the process of thickening began. In another passage, on page 82, speaking of the tracheids of *Pinus silvestris*, he uses the term "primary wall," which, however, is not the same as the first wall laid down in cell division—the middle lamella—but includes the latter as a very delicate layer (*Theilplatte*). The middle lamella differs from the rest of the primary wall in being "cutinized." To the original partition laid down in the process of cell division, Strasburger (**9**) had in 1875 given the name "cell plate."

Treub (**14**), in 1878, studying the living cells of the proembryo of *Orchis latifolia* and the ovules of *Epipactis palustris*, found, after its formation, a splitting of the cell plate, and the deposition of a cell wall between the two layers so formed. This is, I believe, the first suggestion that the median layer of the cell wall is not the plate first laid down in the process of cell division, but is a substance secreted into a space between the daughter cells.

The history of the cell plate theory has been carefully summarized by Timberlake (**13**), and reference may be made to his paper for the literature of the subject. The results of recent investigations go to show the essential correctness of Treub's view. In 1898, Strasburger (**12**) announced that the cell plate splits to form a plasma membrane for each daughter cell. During the splitting process, the rod-shaped elements visible in the cell plate, which represent the material furnished to the plate by the spindle fibers, are pulled out so as to become extremely thin in their middle portion. A middle layer then appears between the halves of the original layer. Whether or not the thread-like portions of the rods persist, either as part of this new layer or as protoplasmic connections between the plasma membranes of the daughter cells, he did not determine. So the question was left open whether the substance of the wall arises entirely by secretion into the space formed by the splitting of the cell plate, or whether a portion of the original cell plate takes part in its formation; but Strasburger has wholly abandoned his old notion of the identity of the middle lamella with the original cell plate.

Timberlake (**13**) finds in the cell divisions of the root tip of *Allium Cepa*, before the appearance of the cell plate elements, an accumulation of an orange-staining substance in the equatorial zone of the spindle. From the staining reactions of this substance, he concludes that it is some form of carbohydrate, probably destined for the building of the wall between the daughter cells. But, while in general the material of this zone stains like the cell wall, it is not stained, as is the wall, by either ruthenium red or iron hæmatoxylin. The cell plate is formed in the midst of this zone by the fusing together of equatorial thickenings of the spindle fibers. The carbohydrate material disappears with the formation of the cell plate, but very soon after the splitting of the plate the young cell wall (middle lamella) appears in the cleft. The cell plate begins to split in its oldest part, that is, in the central portion of the spindle, so that a cell wall may be visible here before the cell plate by peripheral growth has reached the mother cell wall.

Mangin (**3, 4, 5, 6, 7, 8**), in a series of contributions which appeared from 1888 to 1893, investigated particularly the chemical nature of the substance in question. As this side of the subject and Mangin's very interesting conclusions regarding it have been little discussed, a somewhat full résumé of his results may here be given.

Dippel, quoted by Mangin (**3**), had already announced that the new partition deposited by the protoplasm has none of the properties of cellulose. Frémy found in the tissues of fruits and roots a substance called by him pectose, which he was unable to separate from cellulose, and from which are produced the pectic compounds found in the walls of fruits. Maudet found in the pith of certain trees pectose and calcium pectate, forming a cement which holds the cells together. Mangin (**3**) found plant cell walls to be generally formed by the association of two substances, cellulose and one which he provisionally called pectose. In a large variety of adult tissues he found pectose, in a pure state, forming the middle lamella or intercellular substance, and associated with cellulose in the other layers of the cell wall. Dippel's conclusion, that the middle lamella is free from cellulose, was thus confirmed. Some tissues were found to be composed wholly of pectose. It plays the principal rôle in what had been called cellulose fermentation, and Mangin considered chemical modifications of cell walls, as lignification and cutinization, to be due to transformations of pectose, of which cellulose is incapable. At this time (1888) he repeatedly speaks of the pectose layer as the first membrane formed in cell division, the "fundamental layer of the cellular membrane." This seems to indicate an acceptance of the view then held by Strasburger as to the identity of the middle lamella with the cell plate.

But in 1890, Mangin (**5**) suggested the appropriateness of restoring to this layer the name "intercellular substance," as expressing better than that of "middle lamella" its origin and mode of formation. He found it to consist, not of pectose proper, but of a cement of insoluble pectates. To demonstrate the presence of pectic acid, tissues are macerated in a mixture of alcohol and hydrochloric acid, and then treated with a weakly alkaline solution. The tissues dissociate into their constituent cells and fibers, the intercellular substance passing into solution. The solution is shown by analysis to contain pectic acid, which appropriate staining now shows to be absent from the cell walls. In this process, the insoluble pectates are first changed into pectic acid, which, in the alkaline solution, forms a soluble alkaline salt. If sections first treated with acid alcohol are stained with a pectic stain, as phenosafranin or methylene blue, the pectic acid present stains more deeply than the pectic compounds associated with cellulose in the wall layers lying between the intercellular substance and the cell cavity. This indicates that it is not pectic acid and its derivatives, but some of the neutral pectic substances, as pectin or pectose, which are in combination with cellulose in the later deposited layers.

The intercellular substance thus deeply stained forms a thin layer on the whole surface of contact of adult cells; where the cells draw apart, it produces a thick cushion; when the cells separate so as to form intercellular spaces, these spaces are bounded by a pectic layer. This frame of pectic acid is sometimes thickened irregularly, so as to form knobs, points, and sculptures of various forms ornamenting the frame itself or projecting into the intercellular spaces. Sometimes the spaces are partially or completely filled with a jelly-like mass, a soluble transformation product of pectic acid. In the meristem the intercellular layer is not disclosed by staining, but the chemical reactions of cellulose and pectic compounds are given by the cell membranes. That a thin layer of intercellular substance is present is shown by the dissociation of the cells as in older tissues after treatment with acid alcohol and an alkaline solution. Mangin explains the variations in thickness and form of the intercellular cement by its partial transformation in the course of the development of the tissues into soluble pectates; this makes possible the splitting of the membrane, the formation of intercellular spaces, and an exudation of material to form the knobs, points, and other structures already referred to.

A further proof of the presence of pectic compounds in the wall is furnished by treating tissues with a cellulose solvent; the general outlines of the cells remain, the middle lamella, and often a large part, or in some cases all, of the other wall layers preserving their form. The framework thus left takes up pectic acid stains and is indifferent to cellulose stains. The best distinctive stain for pectic substances is ruthenium red, the ammoniacal sesquichlorid of ruthenium. Our knowledge of the value of this subtance is due to Mangin (8), who first described its remarkable properties as a staining reagent for vegetable tissues.

Mangin's attention, it is seen, has been directed to the chemical composition and transformations of the "intercellular substance," and he has not connected his valuable results obtained in that field with a study of its origin. It was in part to supplement his work in this important regard that the present investigation was undertaken.

Strasburger (**12**) and Dippel (**2**) accept Mangin's conclusions as to the widespread presence and the importance of pectic substances in plant tissues, especially in the middle lamella and the thin layer immediately surrounding the intercellular spaces. Dippel's account of the history of the middle lamella in the wood and bast of higher plants is briefly as follows (pp. 570 ff.).

The radial walls of dividing cambium cells are separated from one another by a lax, weakly refractive *Zwischenmasse* or *Zwischensubstanz.* This substance decreases in amount as we pass outward from the cambium layer into the differentiated wood and bast tissues, until it finally disappears, excepting at the angles formed by the junction of three or four cells. Remains of the cambium mother cell walls may occasionally be recognized in the *Zwischensubstanz*, which Dippel believes to be at least partially produced by their disorganization. Chemically, the *Zwischensubstanz* may consist of a union of pectose and callose, which is soluble under the conditions of cell wall development, and so, for the most part, is absorbed into the cambial daughter walls. The cambial cell walls (p. 575), that is the cell walls of the cambium mother[1] and daughter cells, are composed of pectic acid, which, at least after the transformation of these walls into an "intercellular substance," exists largely in the form of calcium pectate. As the cambial daughter cells are transformed into bast and wood tissue, the primary cell walls, consisting of pectose and cellulose, are deposited next to the now apparently simple cambial walls. These latter now undergo a transformation, forming an "intercellular substance," or *Kittsubstanz*, which, through a loss of water and the extension in length of the radial walls, becomes so thin as to be in most cases invisible except after special treatment. It is, besides, fused into apparently intimate connection with the primary cell walls. This combination of the intercellular substance and the primary cell walls forms the middle lamella of mature tissues, against which in the process of development secondary thickenings are deposited. The continued existence of the "intercellular substance" as a middle plate (*Theilplatte*) of the middle lamella Dippel demonstrates by the action of the wall layers upon polarized light, as well as by treatment with various macerating and staining reagents, notably ruthenium red.

Dippel's peculiar view, developed in connection with his studies on the algae, that cell division is accompanied by the formation of a new cell wall entirely enclosing each daughter cell, has doubtless influenced his account of the development of the middle lamella in the higher plants. For if this were the case in the predominantly radial growth of cambium cells, the result would be to leave, between the radial walls of the newly-formed daughter cells, the old mother cell walls, which, if they became disorganized, would form a *Zwischensubstanz* such as Dippel describes. The tenability of this view of the origin of the *Zwischensubstanz* will be discussed hereafter.

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[1] Here there seems to be a contradiction, for Dippel has already spoken (p. 575) of the cambium mother cell walls as being disorganized to form the *Zwischensubstanz* of the daughter cell walls.

MATERIAL AND METHODS.

Woody tissues of the following species were studied: *Pteris aquilina* L., *Pinus silvestris* L., *Nerium Oleander* L., *Rosa* sp., *Tilia Americana* L., and *Ilex opaca* Ait. Of these, Mangin had investigated tissues of Pinus and Ilex.

Free-hand sections were cut, usually both transverse and longitudinal. In many cases, before staining, they were treated for twenty-four hours, as suggested by Mangin (5), with a mixture of one part of concentrated hydrochloric acid and four or five of absolute alcohol, then washed in distilled water. The stains characteristic of pectic acid, especially ruthenium red, are taken up, as a rule, more freely after this treatment, and almost invariably the coloration is more clear-cut and distinctive.

For staining, Grübler's preparations were used. Unless otherwise stated, they were in neutral saturated solution. When an alkaline solution was used, it was prepared by adding to the neutral solution about ½ per cent. of concentrated ammonia solution. Acidulated solutions were prepared by adding a like proportion of acetic acid. In some cases where saturated solutions, *e. g.*, of methylene blue and methyl violet B, were too strong for good results, they were diluted to such a strength that a few seconds' exposure gave a differential stain. Aniline-water-safranin was prepared as directed by Zimmermann (16). An aqueous solution of ruthenium red of a strength of about one five-thousandth was used. An increase in strength above this did not seem to make any noticeable difference in the depth of the stain or in the time of exposure required. This substance is reduced by the action of light in the presence of water, hence the solution must be kept in the dark. It was tried in neutral, alkaline, and acidulated solutions, the alkaline and acidulated solutions being prepared as described for the other coloring matters, substituting hydrochloric for acetic acid. In all cases, the alkaline solution was found to give the deepest and most distinctive colorings, and it is this preparation of ruthenium red that is referred to hereafter. But a few minutes' exposure to the stain is required.

In general, sections after staining were mounted in water and studied immediately. Ruthenium red preparations can be dehydrated by absolute alcohol, passed through clove oil, and mounted in Canada balsam without affecting the stain. But the color gradually fades out from sections so treated, some tissues, notably the xylem and bast, losing their color almost entirely within a few weeks, while others, as the parenchyma and pith, retain it much longer. Sections stained with ruthenium red and mounted in glycerin jelly lose their color almost entirely in the course of a few hours.

Mangin (**4, 6, 7, 8**) has classified the coloring matters used in staining plant tissues, and has described their reactions upon the various substances found in cell walls. Of the great number of stains named by him, the following were employed in this investigation:

Orseille, which colors cellulose in neutral or slightly acidulated solution, but does not affect callose.

Aniline-water-safranin (phenosafranin), methylene blue, Bismarck brown (Vesuvian brown), fuchsin, and methyl violet B (violet de Paris), which do not color callose or cellulose, but do color pectic acid in neutral or acidulated solution. They also color equally well nitrogenous substances (lignin, cutin, etc.), but these may be distinguished by their retention of the color after treatment with alcohol, glycerin, or acids, which treatment decolorizes pectic acid. According to Strasburger (**11**), safranin colors the protoplasmic contents of the cell, the lignified wall, cork, and cutinized membranes cherry-red, the pectic substances orange-yellow. Methylene blue colors the protoplasmic contents and lignified walls blue, the pectic substances violet-blue.

Acid brown, nigrosin, and ponceau, which do not color pectic compounds, but strongly color nitrogenous substances. By mixing one of this series with one of the preceding, Mangin obtained distinctive double stains.

Ruthenium red, which Mangin found the most satisfactory distinctive stain for pectic compounds. It differs from the other pectic stains, as safranin and methylene blue, by the fact that pectic compounds stained by it are not decolorized by glycerin or alcohol. Ruthenium red, he finds, also stains gums and mucilages formed by the decomposition of pectic substances, but does not affect decomposition products of cellulose or callose. Lignified tissues, not stained by ruthenium red when fresh or preserved in alcohol, take it up after treatment with alkalies or Javelle water; but their affinity for ruthenium red is always less than for certain basic organic stains, such as methylene blue, so that by combining its action with that of one of the latter class fine double colorations may be obtained. Cutinized membranes, according to Mangin, are stained in many cases, but not the cuticle. Ruthenium red also stains in varying degrees the protoplasmic cell contents.

PTERIS AQUILINA.

The rhizome was studied in cross section. In unstained sections the middle lamella of the sclerenchyma walls is plainly distinguishable from the inner layers by its greater density and refractive power. It appears as a dark yellowish-brown layer constituting a considerable proportion of the total thickness of the wall, enlarged at the angles where three or four cells abut into a triangular or quadrangular form, often enclosing at such places a similarly shaped intercellular space.

In the walls of the stone cells, while the absolute thickness of the middle lamella is approximately the same as in the sclerenchyma, its thickness relatively to that of the whole wall is of course considerably less. Otherwise its appearance is much the same as in the sclerenchyma. The canals appear as transverse lines seeming to pass quite through the wall, including the middle lamella.

On treatment with methylene blue, the sclerenchyma wall is colored green, except the middle lamella, which, if stained at all, yet appears yellowish-brown in contrast with the other layers. The walls of the fundamental parenchyma, as well as the protoplasmic cell contents, are stained blue. The parenchyma walls are apparently continuous with, and of the same thickness as, the middle lamellae of the sclerenchyma. The green appearance of the sclerenchyma walls is probably not a differential coloring, but is due to a combination of their original yellowish-brown with the blue stain.

In sections treated with ruthenium red, the sclerenchyma and stone cell walls do not take up the stain to any appreciable extent. The walls of the fundamental parenchyma are clearly brought out, and are again plainly continuous with the middle lamellae of the sclerenchyma and stone cells. The indifference of the middle lamella in these thickened walls to methylene blue and ruthenium red, although this layer is directly continuous with the thin, readily-staining parenchyma wall, is in marked contrast to its character in the tissues of the spermatophytes studied; it may be due to a change in the chemical composition of the middle lamella which occurred simultaneously with the deposition of secondary thickening layers. The fundamental parenchyma walls show no evidence of secondary thickening. They are stained by ruthenium red deeply and quite uniformly, save that at the angles the wall is thicker, the triangular or quadrangular area so formed is less deeply stained, and contains apparently a less dense substance than that forming the remainder of the wall. This less deeply stained area corresponds to the thickened corners and the intercellular spaces of the sclerenchyma. The protoplasmic contents of the parenchyma cells are stained unevenly, the nuclei very deeply.

In the vascular bundles, the parenchyma walls are deeply and uniformly stained by ruthenium red. These walls appear continuous with the stained middle lamellae of the large vessels and sieve tubes. In the walls of the vessels the middle lamella is relatively thin; the rest of the wall is uncolored. The middle lamella of the sieve tubes occupies a larger proportion of the wall thickness, the interior unstained layers being very thin. At corners formed by three or four cells the middle lamella appears more dense and somewhat, though not greatly, enlarged.

The staining reaction of the middle lamella in these elements is in contrast to its conduct in the sclerenchyma and stone cells, and agrees with results generally noted in tissues of spermatophytes.

PINUS SILVESTRIS.

Sections of young twigs and branches cut in the fall were used; these, therefore, were past the season of rapid cambial division, and the cambium cells were in a condition of comparative rest. Sections of old and seasoned pine wood were also used for comparison with the young tissues.

In cross sections through the cambium and neighboring tissues of young wood, treated with acid alcohol as above described, the cambium walls are stained throughout their thickness by methylene blue a deep and apparently uniform blue. The result is similar in sections not previously treated with acid alcohol.

Similar cross sections, both in the fresh condition and after treatment with acid alcohol, were stained with ruthenium red. This stain is also taken up freely by the cambium walls. The radial walls are noticeably thicker than the tangential. In the middle of the radial walls there is often a less deeply staining layer, recognizable as Dippel's *Zwischensubstanz.* The rest of the walls are deeply stained, except that in many of the older cambium cells, whose walls are thicker than those of the youngest cells present, there is, next the cell interior, a light line indicating a later deposited, unstained, or less deeply stained wall layer. The corners where radial and tangential walls join are especially deeply stained. In many cases, a continuation of the radial cambium wall into the middle lamella of the xylem and bast can easily be traced.

A difference in depth of stain between radial and tangential walls similar to that given by methylene blue is found in the longitudinal sections treated with acid alcohol and exposed for a few minutes to the action of Bismarck brown.

In cross sections treated with acid alcohol and stained one hour with fuchsin, the cambium walls are uncolored; the protoplasmic contents of some of the cambium cells are stained red. The difference between the affinity of these walls for Bismarck brown and fuchsin is worthy of note; both these stains belong to the class in which a basic coloring matter is united to an acid; according to Mangin, all the stains of this class stain pectic compounds and do not color cellulose or callose.

In unstained cross sections through the xylem, the middle lamella is to be distinguished from the rest of the wall by its different refractive power, at some levels of focusing appearing brighter, at other levels darker, than adjacent layers. The same is the case in cross sections through old pine wood, except that here the middle lamella appears, if anything, more dense than in the young wood.

In cross sections through young wood treated with acid alcohol and methylene blue, the whole xylem is colored green. The middle lamella is distinguishable only by its greater density, as also in sections not previously treated with acid alcohol.

Xylem walls in cross sections treated with acid alcohol stain more deeply with ruthenium red than in sections not so treated. The middle lamella stains much more deeply than the inner layers, the boundary between the lightly and deeply stained portions being sharply marked. The difference in depth of stain is much more apparent in acid alcohol sections than in the others. The tori of the pits in acid alcohol sections are stained deep red; this occasionally occurs also in sections not treated with acid alcohol. In some cases in acid alcohol sections, the torus appears plainly to be a continuation of the middle lamella. In some cases also the middle lamella appears continuous with the interior layer of the pit cavity, which stains deeply. The middle lamella is more plainly differentiated in xylem of the present year's growth. In some preparations the oldest cells of the present year's growth (the spring wood) have the whole wall quite deeply stained. These facts may indicate that it is in the younger xylem walls that pectic substances exist in purest form. Where splitting of the walls occurs in preparing the section, it is sometimes on the line of demarcation between the middle lamella and the less stained layers; very often, however, the split is approximately through the center of the middle lamella. Intercellular spaces occur in the xylem where three or four cells abut; they appear as triangular or quadrangular breaks in the uniformly stained middle lamella.

Comparing the results obtained from methylene blue and ruthenium red, we find that by both the whole xylem wall is stained, the middle lamella being differentiated by the red and not by the blue. Since methylene blue stains nitrogenous substances equally well with pectic acid, and does not stain cellulose or callose, while ruthenium red stains pectic derivatives and not nitrogenous substances, it appears that the secondary layers of the xylem, as well as the thin layer of the cambium wall which does not take up ruthenium red, contain a mixture of nitrogenous and pectic compounds. The use of orseille, a cellulose stain, gave no satisfactory results, showing that celulose, if present at all in these walls, is of minor importance. The staining power of the tori of the pits indicates that they represent in the main the same layer as the middle lamella; this does not, however, preclude the possibility of their also possessing a thin, subsequently deposited layer. The deeply stained layer lining the pits is an example, of which others will be mentioned later, of the possible deposition of a pectic layer very late in the history of the growth of the cell wall.

The relations of the middle lamella, tori, intercellular spaces, and thickening layers appear about the same in older pine wood stained with ruthenium red as in the young tissues already described.

In cross sections previously treated with acid alcohol and exposed for one hour to fuchsin, which belongs to the same class as methylene blue, the xylem walls are stained throughout. Other tissues, except the contents of the cambium and collenchyma cells, are unstained.

Cross sections of older pine wood were left in ponceau solution for three or four days. The xylem is quite uniformly stained vermillion, the middle lamella generally appearing darker than the inner layers of the wall, but the distinction of coloration is not strongly marked, and the difference may be wholly due to the difference in density.

The xylem walls of young wood are not stained after a half-hour's treatment with acidulated nigrosin solution. This fact, by itself, would mean the absence of nitrogenous substances; but, as against that furnished by methylene blue, and by ponceau, which belongs to the same class as nigrosin, such negative evidence is of little value.

In longitudinal sections of young tissues treated with acid alcohol and stained with ruthenium red, the tori of the pits are stained deep red. The appearance of the tori and of the red-staining bars between the pits, which bars are referred by Dippel (**2**) to the remains of the *Zwischensubstanz*, is well shown by him in his figure 397. In many cases, probably in partly developed pits, the stain is only a deep spot at the center. In some cases, an unstained center is surrounded by a stained ring. The pits are not so noticeable where they connect with the cells of the medullary rays, but where the ring appearance just described is found in older wood, the tori of pits so situated are completely stained.

Both the walls and the cell contents, especially the nuclei, of the medullary rays are deeply stained by methylene blue, both in cross sections previously treated with acid alcohol and in those not so treated. This is true of both young and old wood. Similar results are effected by ruthenium red. In cross sections of old wood stained with ruthenium red and then exposed for a few seconds to methylene blue, the red stain of the xylem is replaced by the blue, while, if the action of the blue has not been too long continued, the medullary rays remain red. The greater affinity of the xylem walls for the blue than for the red is due probably to their containing nitrogenous and pectic compounds, both of which take up methylene blue, while the former, unless specially treated, have no affinity for ruthenium red.

In cross sections treated for one half hour with acidulated nigrosin solution, the medullary rays and their cell-contents take up the stain freely.

In cross sections of older pine wood treated for three or four days with ponceau, the medullary rays are unstained.

The readiness with which the walls of the medullary rays take up methylene blue and ruthenium red, and also nigrosin, indicates the presence in them of both pectic and nitrogenous substances. Their preference for ruthenium red indicates a greater proportion of pectic constituents than in the xylem walls. But against this view is the negative evidence of the ponceau, though this, perhaps, is not of much weight.

The cells about the resin pits and their contents, if any, are always deeply stained by either methylene blue or ruthenium red. This indicates, according to Mangin, that the resin and other substances formed in the breaking down of these cells are wholly or chiefly decomposition products of pectic acid and its derivatives.

The staining of the bast is in general similar to that of the xylem. In both acid alcohol and fresh sections, the whole wall takes up more or less freely either methylene blue or ruthenium red, the middle lamella being much more deeply stained than the inner layers. The middle lamella, of course, is thicker relatively to the total thickness of the wall, but is of about the same absolute thickness as in the xylem.

The middle lamella of the collenchyma walls is generally stained more deeply than the other wall layers by methylene blue or ruthenium red, especially in sections treated with acid alcohol. Here, except at the corners, the unstained portion of the wall is very thin, and often the whole wall appears quite uniformly stained. The stain appears more diffuse than in the xylem, and the distinction between the more and less deeply stained layers is not so sharp. The middle lamella is enlarged at the angles of the cells, and sometimes encloses a triangular or quadrangular intercellular space.

The appearance of the collenchyma is very much the same in longitudinal as in cross sections. The collenchyma walls become red when treated for thirty minutes with acidulated orseille solution, indicating the presence of some cellulose, but no distinctive stain for different portions of the wall is observable.

The walls, except the outer ones, of the epidermal cells in either acid alcohol or fresh sections are deeply stained by ruthenium red throughout their whole thickness, but the cuticle remains unstained. This accords with Mangin's results on cutinized membranes.

NERIUM OLEANDER.

Cross sections were cut through growing stems of various ages. The whole of the cambium wall is deeply and quite uniformly stained by ruthenium red either after or without previous treatment with acid alcohol. Similar results are attained by a few seconds' exposure to dilute methylene blue solution. The cambium walls are not stained by an exposure of three or four minutes to acid brown. The middle lamella of the xylem is deeply stained by methylene blue or ruthenium red, the other layers of the wall being colored very slightly if at all. The xylem walls are colored blue by methyl violet B. They are stained quite uniformly brown in a few minutes by acid brown. They are stained uniformly red in forty-five minutes by aniline-water-safranin. After thirty minutes' exposure to this safranin solution the xylem walls are colored bright red, the middle lamellae between the large tubes being decidedly darker than the thickening layers. After forty minutes' exposure to ponceau, the thickening layers of the xylem are stained somewhat, though not evenly, the middle lamella remaining uncolored.

Sections were exposed for twenty-four hours to neutral, acidulated, and alkaline solutions of orseille. The neutral and alkaline solutions produced the same coloration of the various tissues as the acidulated, but to a less degree. Therefore only the action of the acidulated solution will be described. The coloration of the xylem and medullary rays is a purplish-red, of all the other tissues affected, brown. The walls of the xylem have a general purplish tinge, but no distinctive staining is apparent in the different layers. The contents ot the medullary ray cells are deeply colored, and the walls are stained similarly to those of the xylem. An exposure of two and one half hours to ponceau produces a reddish tinge in the xylem walls, and no further stain.

The contents of the medullary ray cells are stained by acid brown. Both the walls and the cell contents are deeply stained by methylene blue as well as by ruthenium red.

The results as to the tissues just described agree closely with those obtained for Pinus. The cambium walls and the middle lamellae of the xylem and medullary ray walls are of pectic nature; the remaining layers of the xylem and medullary ray walls are composed of a mixture of pectic and nitrogenous substances, the pectic constituents being perhaps predominant in the medullary rays; and there is evidence of the presence of a small proportion of cellulose in these thickening layers.

The bast fibers, when treated with ruthenium red, show a peculiar and most beautiful differential stain. It is most clearly brought out after treatment with acid alcohol, though it appears in sections not so treated. The middle lamella, which is relatively very thin, is deeply stained. It is sharply distinguished from the layer next within it on either side, which is colorless or very slightly stained. Next, passing toward the interior of the cell, comes a layer with a little color, then one a little more deeply stained, and so on, the depth of stain increasing until the last thickening layer, reaching almost to the center of the cell, is colored to about the same degree as the middle lamella. It should be noted that the stain shown in these walls is rather a purplish-red than the bright red commonly found in ruthenium red preparations. This behavior with ruthenium red is markedly different from that shown by Dippel (2) in his figure 139, in which all the wall of the bast fibers except the middle lamella is shown as unstained. On page 219, he mentions, as an instance of pectose-free cell walls, the bast fibers of *Nerium Oleander*. This is plainly an error.

The bast fibers are not stained at all by exposure for a few seconds to methylene blue. By methyl violet B (three or four minutes), the middle lamella of the bast and the other wall layers except those next the middle lamella are stained violet.

Acid brown has an effect exactly opposite to that of ruthenium red; that is, the middle lamella is not stained; the next layer is quite deeply colored, the next is lighter, and the colors grow less and less intense until the innermost layers show no coloration at all. After a ten minutes' exposure to acid brown, sections were dehydrated, passed through clove oil, and mounted in Canada balsam, without affecting the staining, except that the color of the bast fibers was somewhat faded. The contents of the bast fibers are deeply colored by acid brown.

The action of orseille (acidulated solution, twenty-four hours exposure) is exactly like that of acid brown. The effect of aniline-water-safranin, on the other hand, is similar to that of ruthenium red.

Exposure to ponceau for various periods up to two and one half hours does not stain the bast.

By treatment for a few minutes with methyl violet B, the middle lamella of the bast and all the other layers except that next the middle lamella are stained violet.

It appears that in the bast, as generally elsewhere, the middle lamella is of pectic nature; that the first of the secondary layers is nearly or quite free from pectic substances, and is composed of a mixture of cellulose and nitrogenous substances, and that the subsequent layers gradually increase in pectic content at the expense of the cellulose and nitrogenous constituents, until the last layer is perhaps again purely pectic. But, from the purplish-red color given by ruthenium red and the indifference shown toward methylene blue, it may be inferred that the pectic compounds found in these walls are not exactly the same as those common to the middle lamellae of other tissues. These inner layers, like the pectic lining of the canals in the xylem of Pinus, show that the ability of the cell to secrete pectic acid is not limited to a single period of its development.

Acid alcohol sections treated for a few seconds with methylene blue show a deep blue color in the middle lamella of the collenchyma walls, much deeper than in the remaining portions of the wall, which, however, are also somewhat stained. The boundary between the middle lamella and the next adjoining layers is not so sharply defined as in the xylem and bast. At the corners of the cells there is an angular, less deeply stained area enclosed by the middle lamella, just as in the fundamental parenchyma of Pteris.

The effect of ruthenium red on the collenchyma is similar to that of methylene blue. The collenchyma walls are not stained by acid brown (three or four minutes), but the cell contents are deeply colored. The contents are also stained brown by acidulated orseille solution, and the walls show a brownish tinge, but no distinctive stain for the different layers. The cell contents are stained by ponceau (forty minutes), but not the walls.

Acid alcohol sections treated for thirty minutes with aniline-water-safranin show a deeper stain in the middle lamella of the collenchyma than in the other wall layers.

The walls of the cork cells are not colored by methylene blue nor by acidulated orseille solution. Orseille also does not stain the cuticle.

In acid alcohol sections the middle lamella of the cork cells is stained more deeply by aniline-water-safranin (thirty minutes) than is the rest of the wall.

The pith cell walls take up ruthenium red freely, the middle lamella, which occupies the greater portion of the thickness of the wall, being deeply stained, especially at the corners. Sometimes the whole wall appears quite uniformly stained. The intercellular spaces are sometimes angular, but very often rounded, elliptical, or circular.

The contents of pith cells are stained by acid brown, the walls unstained. The action of orseille is similar. The failure of these two stains to affect the pith walls indicates that those walls are composed chiefly of pectic compounds, probably in purest form in the middle lamella.

ROSA SP.

In general, the results were the same as for Nerium. Cross sections were treated with acid alcohol and stained with ruthenium red. The cambium walls stain quite uniformly throughout. The xylem shows a distinctive stain for the middle lamella, which is enlarged and especially deeply stained at the angles. The medullary ray walls and cell contents stain deeply.

The middle lamella and successive thickening layers of the bast fibers stain exactly as described for Nerium, including the purplish tinge. The stain of the middle lamella is deepest at the angles. The lining layer of the canals running from fiber to fiber is deeply stained where it traverses unstained or less deeply stained layers. This recalls the deeply stained layer of the pits of pine tracheids, and, with the deep stain of the last deposited wall layer in these tissues of the rose, shows these cells to possess the power very late in their history of depositing pectic wall material.

The pith cells show a very distinctive stain for the middle lamella.

In the collenchyma, the walls are stained throughout, the middle lamella much more deeply than the other layers, but the boundary between more and less deeply stained portions is not so clearly defined as in the xylem. The epidermal walls are stained about the same as the collenchyma. The cuticle is unstained.

Cross sections of a slightly older stem than that just described were stained with ruthenium red, then exposed for a few seconds to methylene blue. The xylem walls are stained purple by the combination, the middle lamella most deeply. The bast fibers take up both stains, the relative depth of stain of the various layers being about the same as with the red alone. The epidermal walls take up the blue more freely than the red. The collenchyma cells remain red.

Cross sections of a very young growing shoot were treated with acid alcohol and stained with ruthenium red. The cambium walls stained deeply throughout. Very thin tangential red lines are visible, representing the earliest deposit of wall material. Such very thin tangential walls are what one would expect to find in material gathered in the season of active cambial growth.

Young xylem elements have the walls entirely stained, showing a long-continued period of pectic deposition. In older fibers a middle lamella is deeply stained, the remaining layers very slightly or not at all.

The bast fibers are stained throughout; no thickening layers are yet distinguishable. The middle lamella is already differentiated in the collenchyma, the other layers remaining uncolored. The middle lamella is especially deeply stained in the corners, and angular intercellular spaces are in some cases inclosed by it.

Similar sections not treated with acid alcohol yield similar results.

TILIA AMERICANA.

Cross sections through rather young growing shoots were treated with acid alcohol and ruthenium red.

The cambium walls stain deeply, in the youngest cells throughout their entire thickness. The radial walls are more deeply stained than the tangential, the corners especially deeply. Passing from the youngest cambium cells toward the bast or toward the xylem, the beginnings of the secondary thickening may be seen in a very thin unstained or only slightly stained layer of the wall within the stained portion. This is similar to the behavior of the cambium walls of pine, except that in Tilia, as generally, there is no evidence of a *Zwischensubstanz*, which, so far as I have observed, is found only in the pine cambium walls. The continuation of the deeply stained layer can be traced in the middle lamella of the much thickened xylem and bast elements.

The middle lamella of the xylem stains deeply, especially at the angles, where it is enlarged. The rest of the wall is slightly tinged with red.

The contents of the medullary ray cells are stained. Their walls are more uniformly stained than those of the xylem elements, but the middle lamella is still plainly distinguishable.

The bast has a deeply stained middle lamella, the other layers of the very much thickened wall being unstained or only slightly stained. In this respect, as in most others, the staining reactions of Tilia resemble those of pine.

The walls of the parenchyma cells between the bast bundles show a stain throughout, the middle lamella appearing thin and deeply stained, and somewhat enlarged at the angles.

In the collenchyma the whole wall and the cell contents are stained. Here, too, the middle lamella is thin and deeply stained, often including at the angles a less deeply stained area.

The walls of the cork cells stain quite uniformly throughout, but not very deeply. The color is purplish, different from the bright red typical of the middle lamella in other tissues. No middle lamella is here distinguishable. If anything, the innermost wall layer, next the lumen, is most deeply stained. Here, as in some of the tissues of Pteris, there is evidence that the middle lamella has undergone a chemical change, some or all of its pectic content having been replaced by other substances. The cuticle is unstained.

ILEX OPACA.

The tissues of the holly resemble those of the pine in their reactions to ruthenium red, the only stain I have used upon them.

In cross sections, either with or without previous treatment with acid-alcohol, the cambium walls are stained throughout by ruthenium red, and their connection may be traced with the middle lamellae of the xylem and bast.

The middle lamella of the xylem is thickened at the corners and stains deeply; the rest of the wall stains but slightly.

The middle lamella of the pith, which takes a deeper stain than the rest of the wall, is thickest at the angles, where it frequently encloses intercellular spaces. These spaces are sometimes triangular or quadrangular, but usually with more or less rounded angles, and often of an elliptical or circular form.

The middle lamella of the bast stains deeply, the rest of the wall slightly. The same is true in the collenchyma walls, where frequent angular intercellular spaces occur. The walls of the cork cells show no stain.

DISCUSSION.

In almost every tissue studied in which there was evidence of the deposition of wall layers at different periods, the staining reactions of the middle lamella showed it to differ in chemical composition from the adjoining layers; my results confirm Mangin's in every respect upon this point. Its distinctive character was brought out most clearly by ruthenium red. The reasons for concluding that, in general, this peculiarly staining layer is composed of pectic acid and its derivatives, have already been given at length. It does not follow, however, that its chemical composition is unchangeable. On the contrary, it is clear that, during cell growth and development, changes occur in the chemical constitution as well as in the form and mass of the middle lamella.

In pointing out the existence of a *Zwischensubstanz* between the radial walls of the cambial cells, and in distinguishing this layer from the "intercellular substance," either as characterized by Mangin or by himself, Dippel has contributed essentially to our clear conception of the conditions in the cambium of the pine; but his notion that the *Zwischensubstanz* is derived from the walls of the cambium mother cells has little evidence in its favor. I have never seen in this mass the fragments of these walls of which he speaks (**2**, p. 575). Besides, were Dippel's view correct, the tangential walls would be expected to contain at least as much of this substance as the radial walls; but, in fact, nothing of the sort is to be seen between the tangential walls, which, however, as shown in Dippel's own figures, are no thicker than are the radial walls without the *Zwischensubstanz*. On this point of the origin of the *Zwischensubstanz* Dippel is not clear, for he distinctly says (p. 575) that it is derived from the degenerated cambium mother cell walls, and again, on the same page, he speaks of the latter as going to make up the intercellular substance. It seems to me more probable that this *Zwischensubstanz* represents pectic acid which has exuded through the cambium cell walls into an intercellular cleft formed by the splitting of the radial walls, and that it is analogous to the lax substance sometimes found at the angles of cells before the appearance of empty intercellular spaces. Its ultimate fate is doubtless to be absorbed into the adjacent cell walls, so that it does not appear as a visible layer in the middle lamella of mature tissues except in the case of the areas represented by the red-staining bars of the pine tracheids (see Dippel's figure 397), and except also, perhaps, on the surface of intercellular spaces. The intercellular spaces of the pine wood, then, are to be interpreted as remnants of the radial clefts between the cambium cells, rather than as newly formed in the adult tissue. But this does not preclude the probability of changes in the form and extent of the spaces due to the rounding up of the adjacent cells. It would be interesting to know whether this *Zwischensubstanz* is of wide occurrence. I have not observed it elsewhere than in the pine, and Mangin does not specifically note its existence.

A fact which is important as showing the plastic nature of the middle lamella at an early period of its history is its variation in thickness in different portions of older walls. This is shown commonly by an enlargement at the angles and a decrease in proportional thickness at the sides of the cells. Such variation is in marked contrast in the spermatophytes studied to the practical uniformity in thickness of the completely stained cambium walls. These are continuous with the middle lamella of the differentiated tissues, and, were it not for this change in form, would appear identical with the middle lamella. In some of the tissues examined, the substance of the middle lamella appears more dense at the enlarged angles, and seems to take up the characteristic stains more freely at those places. This appearance, however, may be accounted for by the optical effects produced by the greater thickness at the angles. But in other cases, as in the fundamental parenchyma ot Pteris and the collenchyma of Nerium, these enlarged angles enclose a less deeply staining substance, or are becoming empty. These may be considered as stages in the development of the intercellular spaces, which are located, like the areas of less deeply stained substance just mentioned, at the angles formed by the junction of three or four cells, are enclosed within the apparently split middle lamella, and are commonly angular in form.

Since there is no trace, except in the pine, of a *Zwischensubstanz* whose absorption would leave intercellular spaces, such spaces in the tissues of other plants can be accounted for only by the rounding up and drawing apart at their corners of adjoining cells. This induces a splitting of the middle lamella. The cleft so formed may be temporarily filled by a lax, fluid or semi-fluid substance, a solution, perhaps, of pectic acid or one of its transformation products, but this in time is absorbed into the walls, leaving an empty space. The surfaces of the wall exposed to the so-formed intercellular space may become further modified chemically, and even so softened as to flow enough to form a rounded instead of an angular space; but there is no evidence that such chemical changes ever occur except where the wall is exposed in an intercellular space, and it is more likely that the plasticity here displayed by the pectic acid has characterized it from the time of its deposition, but has not been shown so plainly because of its confinement within comparatively rigid limits.

On the basis of the later investigations respecting the relation of the cell wall to the cell plate, we have seen that the middle layer appearing after the splitting of the cell plate is to be considered as formed by deposition from the split halves of the original plate; the middle lamella of mature tissues would include, then, in addition to possible later deposits, both the layers deposited on the inner surfaces of the daughter plasma membranes. This being the case, we might expect to find in the history of the development of the middle lamella evidences that it consists of two layers. This is just what is found in the case of the intercellular spaces, which are very evidently caused by a split through the center of the middle lamella. If the middle lamella were not of a double nature, we should hardly expect it always to split through the middle, but, in view of its marked difference from the adjoining layers, we should expect that sometimes the whole layer would be pulled to one side or the other as the cells round up and draw apart at their corners. As noted above, in sections split in cutting, there were also frequent cases where the middle lamella split rather than tore away from the other layers. The splitting in all these cases seems to indicate a weakness of cohesion in the plane between the two layers first deposited by the plasma membranes; and confirmation is thus given of the view advanced by Strasburger and confirmed by Timberlake that the cell plate splits before the new cell wall is laid down, the latter thus having a double nature from the start. We should not overlook the possibility that the very first layer which appears between the daughter plasma membranes is so thin as not to form a noticeable fraction of the thickness of the mature lamella; and that the splitting at a later stage in the middle lamella's history is due to a decomposition of this first thin layer, or that the split is really on one side or the other of it. I have, however, seen no evidence in support of either of these hypotheses.

It cannot be supposed that the middle lamella consists only of the material first deposited from the young plasma membranes. Its thickness in adult cells, and its varying thickness in different tissues of the same plant, *e. g.*, the large vessels and the sclerenchyma of Pteris, at once negative such an assumption. The older view, that it was the cell plate directly metamorphosed into cell wall material, is just as effectively negatived by the same considerations, which should have had more weight with the earlier observers. The middle lamella is rarely difficult of differentiation in adult thick-walled tissues simply by its greater density and less apparent stratification. Moreover, its growth in thickness can often be traced, for it stains continuously from the youngest wall (the thin tangential red lines in the cambium of the rose) to the middle lamella of mature tissues. We must conclude that the middle lamella consists of the layers first deposited by the plasma membranes *plus* a certain amount of material subsequently deposited in contact with these layers, which is generally rich in pectic compounds as compared with still later deposited strata. The middle lamella may vary considerably in thickness in different tissues, according as a greater or less amount of material rich in pectic substance has been deposited in the cell. That it is not the only part of the cell wall, however, that contains pectic compounds is shown from the taking up by the other layers of the wall, though less freely than by the middle lamella, of pectic acid stains; it is shown also in the pectic layers lining the pits of the pine and the canals in the bast fibers of the rose, and in the innermost thickening layers of the bast of Nerium and rose.

Although the middle lamella usually retains its pectic nature, it undergoes a change by which, in the course of cell development, it loses the power of adapting itself to the varying form of the adjoining cells and becomes fixed and inflexible. The evidence seems satisfactory that this change, as Mangin suggests, is one from pectic acid to insoluble pectates, chiefly the calcium salt. Such a change is indicated by a less deep staining in older tissues, unless they are first treated with acid alcohol. A further transformation appears to take place in the cork cells of Tilia, by which the power of distinctive staining is entirely lost, and the middle lamella cannot be distinguished from the other layers of the suberized wall. The pectic acid here seems to have been partly replaced by suberin. The coloration of the cork walls is purplish, indicating a possible similarity in chemical nature to the later layers of the bast elements in Nerium and rose. In the sclerenchyma and stone cells of Pteris, also, though a middle lamella is plainly present, its staining reactions do not distinguish it from the rest of the wall; yet it can be traced as a continuation of the thin, characteristically-staining walls of the fundamental parenchyma. It is possible that the middle lamella in this case was from the start non-pectic; but it seems more probable that, as secondary thickening proceeded, the pectic acid was replaced or masked by material similar to that deposited to form the other layers. Further light could be thrown upon this question by tracing the development of the wall from the meristem to the mature tissues. The difference in depth of stain between radial and tangential walls in Tilia may indicate that the tangential walls in this case are not composed of pure pectic acid, or that it exists in them in a somewhat different form. Such a difference in chemical nature might easily occur, since the tangential walls are being laid down anew, while the radial walls are older, and at most are simply added to as the cells increase in number and size. There is no evidence of the existence here of a mass corresponding to Dippel's *Zwischensubstanz.*

The power of the cell to secrete cell wall materials of very different chemical composition at different periods in its history is much greater even than is indicated by Mangin's work. That the compounds stained by ruthenium red are not derived from the decomposition of a previously deposited cellulose wall is proved by the complete staining of the young cambium wall. Still, that there is a possibility of a closer relation than Mangin supposes between cellulose and other cell wall materials on the one hand, and pectic substances on the other, perhaps even involving transformations of material from one class into the other, is to be inferred from the action of ruthenium red upon the walls of the cells surrounding the resin pores in pine. But that the power of secreting pectic compounds is not limited to a single period in the history of the cell is shown by the changes already discussed in the mass of the middle lamella. Since the very youngest and thinnest cambium walls are stained by ruthenium red, and at a later stage the thicker walls are still completely stained, the power of depositing pectic acid must last for a considerable time. That it continues in some cases even beyond the cambium stage is indicated by the variations in the thickness of the middle lamella in older tissues. Pectic substances, though perhaps not in the form of pectic acid, are also secreted at later stages in cell wall development, usually in combination with other materials, as cellulose, callose, and nitrogenous substances. In most of the thickened walls studied, evidence of the presence of pectic substances was found in the secondary thickening layers. The general rule, that pectic compounds are deposited in the cell wall early in the life of the cell, and that layers deposited later are predominantly non-pectic, is seen to have exceptions in the case of the innermost strata of the bast fibers of Nerium and rose, and in the lining of the canals of the rose and of the pits of the pine. In these cases we have the deposition first of a pectic layer, then of non-pectic or mixed layers, and then again of a pectic layer. The purplish tinge imparted to the bast thickening layers just mentioned by ruthenium red indicates that these layers consist of some pectic substance or substances, other than pectic acid, at least in the form in which it exists in the cambium walls and the middle lamellae of other tissues.

Whether the period during which the cell generally deposits pectic acid, and thus forms the middle lamella, marks any special stage in its development which can be sharply distinguished from subsequent periods in its history is not certain. The evidence at present available seems to indicate that the pectic layer continues to increase in thickness about as long as the cambial cell is increasing in size. It is possible that the attainment by the cell of its adult size marks the limit of the growth of the middle lamella. In this case we might say that pectic acid is deposited so long as the metabolic processes of the cell result in a *plus* which is expressed in cell growth, but that later, when a metabolic equilibrium has been established, or when the excess of food is stored instead of being used for growth, or when the protoplast degenerates, a predominance of other cell-wall materials is deposited. The evidence for such a view, however, is far from complete. It must be remembered, too, that in the cambium cells the distinction between middle lamella and inner non-pectic layers is very early present, and that the middle lamella continues to increase in thickness after it is separated from the protoplast by the non-pectic strata deposited later. The middle lamella is not to be considered as consisting merely of the wall layers early deposited by the protoplast, without undergoing any later modification. It is quite possible that the pectic acid which characterizes it may in part be secondarily formed or deposited by infiltration through non-pectic layers which separate it from the protoplast. Some such hypothesis as this is necessary to account for its increase in thickness during the later stages of cambial growth. Of interest upon this point is the fact noted by Mangin that, although in the meristem of some of the plant tissues studied by him no middle pectic layer could be detected by staining, yet, upon a treatment known in other cases to dissolve pectic acid, the cells are dissociated. My study of very young rose shoots, though not carried back far enough to dispute Mangin's results, yet shows that, at a point where the tissues have become very slightly differentiated from the meristem, the cambium walls show strongly by their affinity for ruthenium red their pectic nature.

CONCLUSIONS.

The facts that have been cited seem to me to show conclusively that the middle lamella is not merely the partition wall first laid down, either as a single or a double layer, by the plasma membranes. Nor is it, on the other hand, merely an intercellular substance of cement, a means for binding the cells together, as Mangin holds. Individual cells are not separated from one another, either in their formation or their later development, and no reason appears why an intercellular cement should be secreted. There is, however, abundant reason why, in woody tissues especially, there should be during cell growth a plastic region in the cell wall, which should be in a measure adaptable to the changing size and form of the protoplast itself, and to the firm, resistent layers whose form must correspond to that of the protoplast at the time of their deposition. The middle lamella is, therefore, a wall layer with a complicated history, undergoing after its first appearance changes in form, increase, and probably at times decrease in mass, and changes in chemical composition; its history, too, is not identical in different tissues. There can be no doubt that, in the higher plants studied, the young cambium walls are included in, and form the basis of, the middle lamella of the older tissues. These may at first include, at least in the pine, an amorphous *Zwischensubstanz*, which occupies a cleft formed by the splitting of the young radial walls. Quite early in the history of the cambium cells, a non-pectic layer appears within the first-formed pectic stratum; but the latter, now properly a middle lamella, continues to increase in thickness even after the appearance of the non-pectic layer. The substance of the middle lamella, now, is not rigid, but is more or less plastic, or even, as Dippel believes, soluble under certain conditions of development. Its solubility may lead at times to its partial absorption by the rest of the wall. More often, probably, its mass is increased by further secretion of pectic material from the adjoining cells into the spaces formed by their rounding up. The plastic nature of the whole layer allows the modification of its shape, also, as the cells round up and as more resistent layers are deposited against it, leading to its being massed at the corners and pressed out to a thinner layer at the sides. The pressure may be in certain cases so great at the corners as to increase the density at those places; but in general, as the cells round up and draw away from the corners, the pressure there is relaxed, and, if new material is not deposited, the substance becomes less dense, perhaps swelling by the absorption of water. Or it may be that already the middle lamella has split, and the cleft has been filled by the exudation into it of a pectic fluid, which is later to be reabsorbed. At any rate, sooner or later the tension incident to the rounding-up process brings about a split in the middle lamella, and an intercellular space is formed. In case a *Zwischensubstanz* was present, a splitting at this time is unnecessary, and the intercellular space results from the absorption of this substance. If the substance of the middle lamella is sufficiently rigid, the intercellular space remains angular; but if the material still retains some plasticity, or if it undergoes a chemical change upon its exposure at the newly formed surface, the angles may be rounded, or may disappear entirely, leaving a circular or elliptical space. The chemical changes effected in the middle lamella after the cell has attained its final form consist in the conversion of pectic acid into insoluble pectates, or even, as in the cork cells of Tilia, its replacement by entirely different substances.

It seems to me plain that the term "middle lamella," indicating merely the position of the layer in question, is preferable to either "cement" or "intercellular substance." The latter term, arising from a totally false conception as to the origin of cells, should certainly be dropped. There is also no evidence that the cell wall layers which, taken together, form the middle lamella have any significance as a cement for binding the cells together, and so it is inappropriate to apply to them a name suggesting any such function.

The fact of the origin of the middle lamella as a double layer deposited on the surfaces of two plasma membranes, and the fact that in the formation of intercellular spaces it always splits in a median plane, must always be borne in mind. This constant plane of cleavage may be called the primary cleavage plane, or, perhaps, the primary cleft when it is spoken of with reference to the space between the daughter plasma membranes in which the cell wall material is deposited.

I would distinguish cambial walls as the walls of cells yet capable of division, and primary cell walls as those layers added during the growth of the cambium cell into a full-sized wood or bast element. Secondary thickening would include the strata deposited in the subsequent history of such cells. This secondary thickening may be subdivided further where evidence exists that its deposition has been interrupted and subsequently resumed; we should then have tertiary thickening, and so on.

For the adult condition of thickened cell walls, the following terminology might be proposed as most exact from the standpoint of our present knowledge:

The boundary plane between adjacent cells, commonly invisible except where indicated by intercellular spaces, would be, following the suggestion already made, the primary cleavage plane. Including this on both sides, we should have the apparently homogeneous middle lamella, including the cambial walls and more or less of the primary cell walls, according to the proportional pectic acid content of the latter. Then would come those layers of the primary wall, if there be such, which are predominantly non-pectic; and lastly the layers of secondary and perhaps tertiary thickening formed in the metamorphosis of the adult cell into its permanent condition as the element of a tissue.

The investigations here discussed were undertaken at the suggestion of Professor R. A. Harper, and have been carried on under his direction. All the results accomplished are due in the highest degree to his suggestions and assistance.

UNIVERSITY OF WISCONSIN.

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STRUCTURAL STUDIES ON SOUTHWESTERN CACTACEAE.

CARLETON E. PRESTON.

(WITH NINE FIGURES)

THAT the Cactaceae, a family in every respect appearing to be of recent origin, are unique in the extent of their adaptive modifications to arid conditions is a commonplace. Not only does this adaptation affect the external parts as gross structures, but in still greater measure does it work changes upon the minute anatomy by modifying the histological elements. These internal changes, keeping pace with and supplementing the external, raise this family to the first rank among the desert plants. A critical study of the minute anatomy from the standpoint of ecology, therefore, should be most fruitful. Moreover, since the family is one of late origin, in which definite groups have so far not crystallized out, but between which nearly all connecting links are present, a general comparative examination of internal structure should afford at least some further clue as to the lines upon which the various groups have developed or are still developing, adding to or confirming the evidence already obtained from the study of external characters.

Viewed from the standpoint of the systematist, this paper, being a study of the general histology of eight southwestern forms, can by itself be of little value, serving only as an addition to the number of species already critically examined. Although in collecting the material for study it was my intention to choose such forms as could be considered typical, I found, as work went on, that too much variation occurs to admit of their use in this way except upon the broadest lines. In order to do complete and satisfactory systematic work on the basis of structural characters, evidently one would have to compare, not only all the genera within the family, but at least the larger subdivisions and the doubtful species in each genus. The single genus Cereus contains a multiplicity of forms, the structures of which must be very diverse. How are these related, and what are their several connections with the other genera? Does the gradual change in internal structure agree with the external and strengthen the validity of the various systematic groups as now recognized? Schumann[1] has pointed out that the original ancestor of the Cactaceae was probably something like Peireskia. Ganong[2] has followed up and confirmed the relation between this genus and Opuntia, chiefly on the basis of external characters. What are the steps by which the corresponding internal structure has changed? Schumann[1] has hinted rather strongly at the connecting links between Opuntia and Cereus; anatomical studies may give more definite information upon this point.

This paper seeks to impress the importance of careful structural study to help out the ordinary work on external characters, to point out the general trend of evolution exhibited, and to interpret certain anatomical conditions upon a physiological basis.

As regards environmental adaptation, next to diminution of surface and other modifications to lessen transpiration, the storage of water is most important. The turgor exhibited in many of the more succulent forms is surprising. Especially is this the case in the younger portions of the arborescent species, and throughout the interior of those which are low and cespitose, where for a long time turgor alone is sufficient to sustain all the weight placed upon it—in other words, to preserve the rigidity of the plant. Hence there is no necessity for a strong vascular system; in fact, its room is more valuable than its presence, and we find in general that the vascular system is of late development, and in low forms almost never reaches a high state of perfection. The component elements also are oftenest of a kind generally considered primitive, showing an apparent retrogression, but one which in many cases is complicated by the addition of adaptive modifications. This is true particularly in the first form examined, *Cereus Fendleri*, of cespitose habit, and one of the most succulent. Upon cutting a shoot transversely one will notice that the bundles recede into the tissue for some distance, both in the severed portion and in that remaining on the plant, while the parenchymatous tissue still remains turgid. It is thus easily demonstrable that the bundles are normally under great tension. The mechanical arrangement by which such elasticity is rendered possible will be found in the structure of the xylem. Another point of interest, probably of value upon systematic grounds, is the behavior of the bundles in the matter of secondary medullary ray formation, development of interfascicular cambium, and anastomosis.

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[1] Gesammtbeschreibung der Kakteen. 1897.

[2] Beiträge zur Kenntniss der Morphologie und Biologie der Kakteen. Flora **79**: 49–86. 1894.

Before considering the various forms separately, there are certain points of structure which can best be mentioned in general. Schumann, both in his monograph and in Engler and Prantl's *Pflanzenfamilien*, gives an idea of the ordinary structure of the group. A condensed account is also given by Ganong[3] which I take the liberty to quote as a basis for the following discussion.

> As to the tissues, it is enough here to say that the characteristic xerophilous appearances are a strong cuticle, thick epidermis, perfect cork, sunken stomata, collenchymatous hypoderma, deep palisade layers, great development of pith and cortex, which consist of large, round, splendidly-pitted water-storing cells, often containing mucilage; a fibrovascular system, in general simple in its make-up, lacking annual rings, composed as to its xylem of strongly-ringed and spiraled tracheids, which are often collected into gland-like masses, the whole system conforming closely to the external form and following its morphological changes.

Regarding the character of sunken stomata and their relation to hypoderma slight comment is necessary. The stomata are not sunken in the sense of having deep-lying guard cells; on the contrary, they are well upon the surface, as Schumann notes. Whatever vestibule there may be is of a different nature. With the increase in thickness of hypoderma an interval is produced between the assimilative tissue and the guard cells. Through this collenchymatous tissue run canals connecting the two; these canals must at all times be filled with water vapor, and probably act in a much more effective manner than would an equally large external vestibule. The hypoderma is of varying thickness, of one cell layer only in some species of Mamillaria, of seven to ten in certain other forms, as in *Cereus giganteus*. There appears to be no difference in the character of the cells in the various groups; the walls are irregularly thickened, the thin portions allowing osmotic transfer of materials between the cells, and from them to the epidermis. Portions of hypoderma are shown in *figs. 1–3*.

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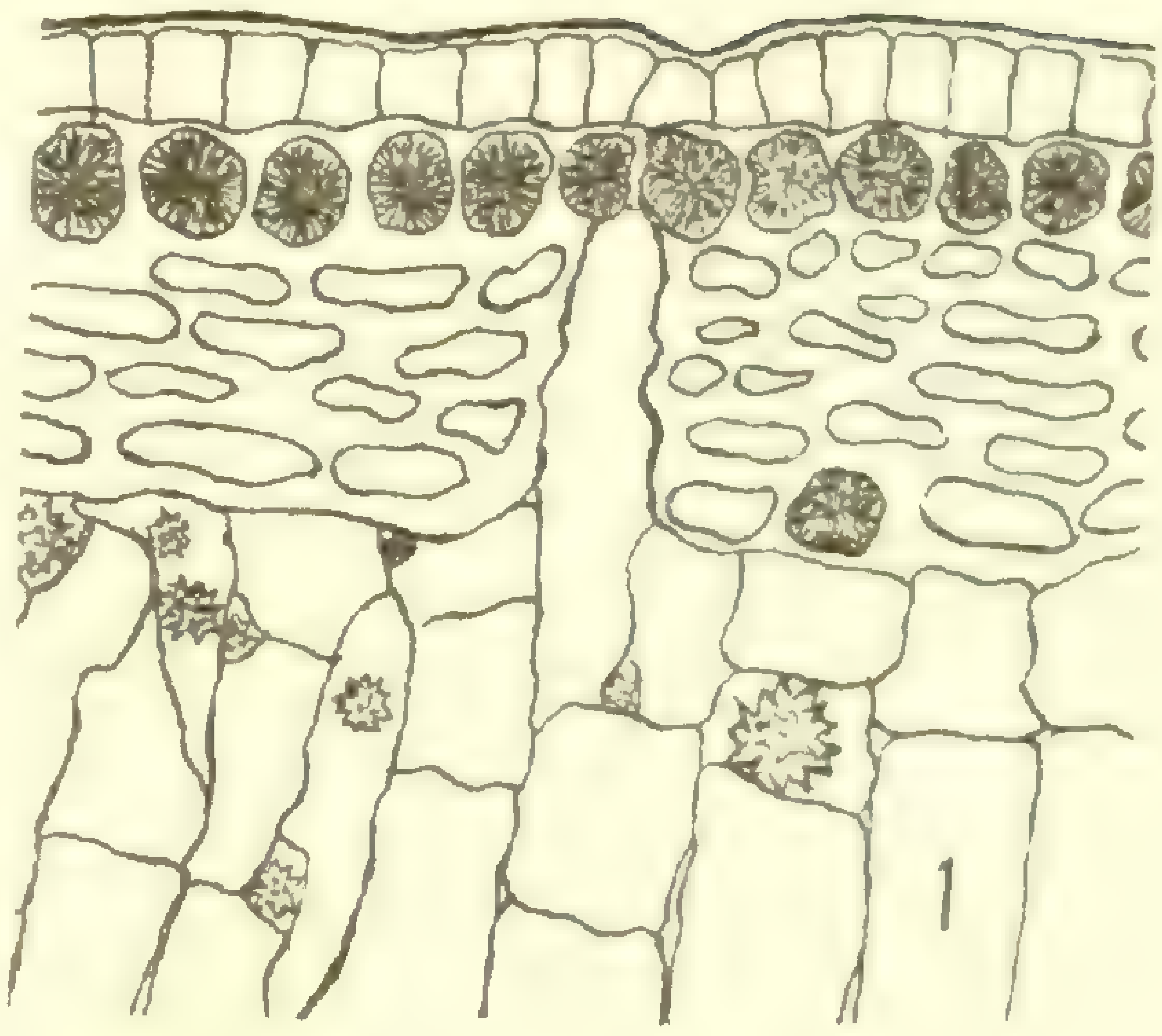
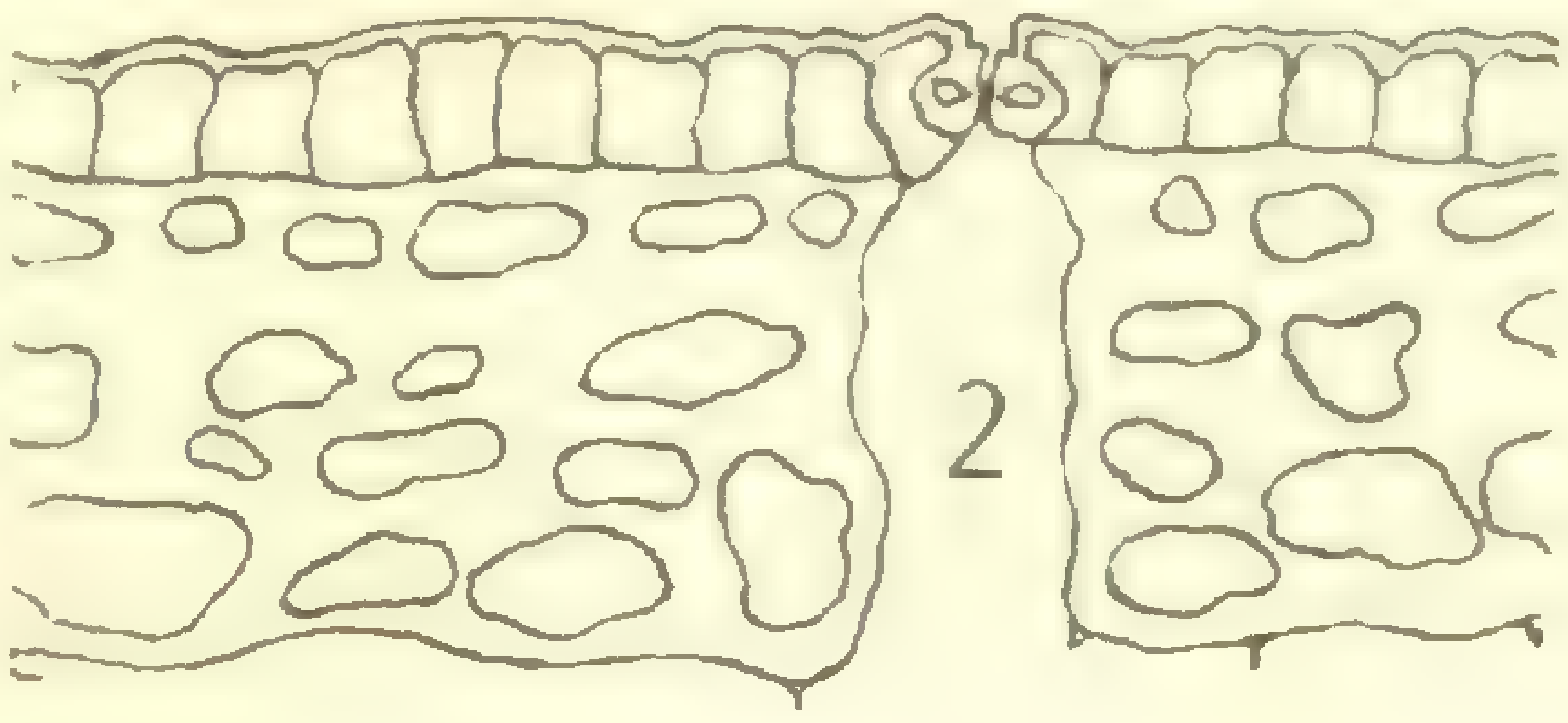
[3] Recent problems in the anatomy, morphology, and biology of the Cactaceae. Bot. Gaz. **20**: 130. 1895.

With respect to assimilative tissue, Ganong speaks of deep palisade layers. Schumann, on the other hand, says that the cells are not in palisade form, but spherical. In point of fact, there seems to be considerable variation in this regard. In no form which I have examined have I found an assimilative tissue of absolutely spherical unmodified cells. There has always been an elongation perpendicular to the surface, sometimes slight, as in *Opuntia leptocaulis*, in other cases very well-marked, as in *Echinocactus Wislizeni*. There is also a general compacting of the tissue in this region. These elongated cells extend inward in the form of more or less definite chains or filaments, grading rather slowly into the ordinary parenchyma tissue, which in many cases contains chlorophyll in some quantity, in others is colorless. In the latter instance the chlorophyll, as noted with the naked eye, seems confined to a well-marked rind.

It is perhaps only fair to suggest that environment may have a considerable influence upon the development of the palisade form in this family, as well as in those which possess functional leaves. The classical works of Stahl, Pick, and other investigators leave little question but that the elongation of the assimilative tissue, at least in some degree, is in direct response to the stimulus of light. The habitat of the plants here described and contrasted is one marked for its great light intensity, which, as I have found from a rather comprehensive examination of foliar structures, leaves its imprint upon the arrangement and development of assimilative tissue in almost all cases. Schumann's statement that the assimilative cells are spherical may be true of the plants when a general average is taken, including epiphytic types, and others growing under entirely different light conditions. Possibly also the effects of artificial cultivation may have some place in his results.

The medulla in many cases is of thick-walled and pitted cells, as Ganong describes, but this is by no means universal, often varying within the limits of a genus as now established. The cells are often exceedingly thin-walled and have no need of pits to maintain connection between them. The presence in this tissue of mucilage, crystals, etc., is likewise variable with the species, and needs separate discussion. Not only do the crystals vary in distribution to a wide extent, but also in relative frequency, some species being far richer in this deposit than others of the same habitat, a fact which, it seems to me, can only be referred back to the varied selective power of roots for chemical solutions.





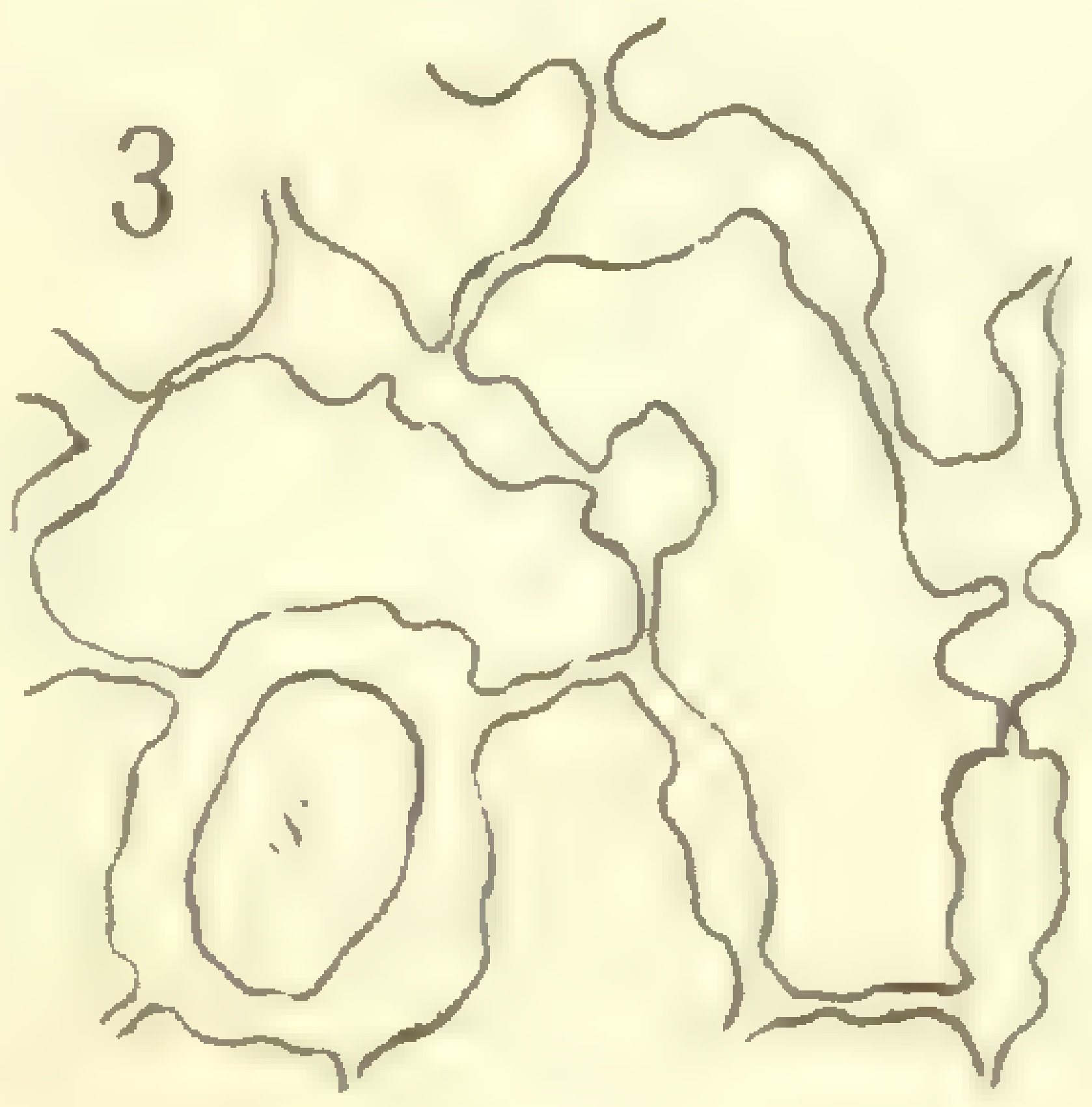


FIG. 1.—Epidermis and hypoderma of *Opuntia arbuscula;* opening of stoma does not show, owing to slightly oblique character of section.

FIG. 2.—Epidermis and hypoderma of *Cereus Fendleri* in section, showing stoma.

FIG. 3.—Hypoderma of *Cereus Fendleri*, seen from inside, showing character of walls and opening of stoma canal (*s*).

The particular value of Ganong's terse and concise description of the fibrovascular system lies in the last clause, "the whole system conforming closely to the external form, and following its morphological changes." Upon this fact depends the usefulness of internal structure as evidence of systematic value, a point which this writer thus recognizes, and one which I feel that I cannot too strongly insist upon. Schumann gives a slightly fuller account of the vascular system, noting the presence of annular and spiraled ducts, *especially in young bundles*, and their subsequent replacement by the various tracheids. This is also the statement of the fact that a regression toward more primitive conditions is taking place, by the substitution of elements of a less highly developed character. In this particular especially considerable variation is shown, offering, together with the methods of bundle-branching and anastomosis, a very fruitful field for research from a systematic point of view. Annual or periodic rings are not always absent, as will be shown ; in fact, in one form I have examined they are peculiarly marked.

The work presented in this paper was done on fresh material collected in the vicinity of Tucson, Ariz., during December 1900, and examined immediately at that place. Opportunity was thus given to study the plants in their natural habitat, a very valuable advantage in dealing with physiological phenomena.

CEREUS FENDLERI Engelm.—The hypoderma is comparatively thin, of about three layers of cells ; the cuticle is thick as usual ; there are no crystals in the epidermis, only an occasional one occurring in the deeper cells of the hypoderma. The assimilative cells are large and fairly elongated, those nearest the surface containing the most chlorophyll, those toward the center grading into a very thin-walled parenchyma also slightly chlorophyllous, and filled with an intensely stringy and slimy mucilage, which, by taking stains readily and by preventing dehydration, renders any delicate manipulation of sections upon fresh tissues out of the question. It is by this means that the plant is able to hold water so persistently. In the parenchyma are imbedded the bundles, slightly separated from each other in most cases, but with some anastomosing. The lateral branches, which apparently start for the tubercles, break up and form a network through the tissue. In this species the bundles appear to start in a definite circle in cross section, in contrast to the undulate line in which they occur in certain other forms. There seems to be no interfascicular cambium, the bundles in their exceedingly slow growth apparently pushing their way outward into the succulent tissue, compressing it about them, and taking up the room it formerly occupied, instead of the growth of the medullary tissue keeping pace with the increase of the bundles. The development of phloem is exceedingly slight, consisting wholly of sieve tubes and companion cells, with no trace of thick-walled elements.

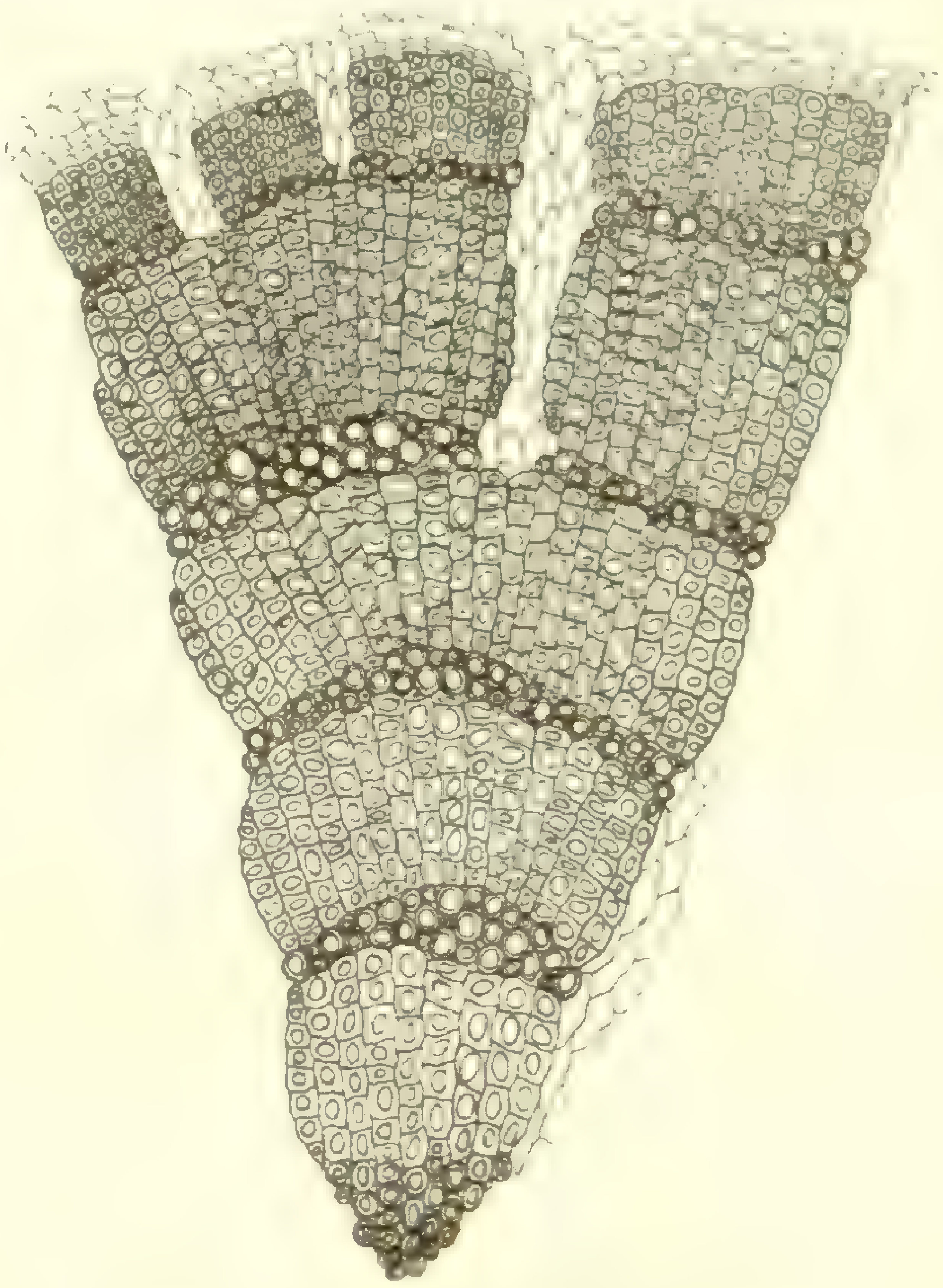


FIG. 4.—Xylem portion of stem bundle in *Cereus Fendleri.*

Of the xylem more needs to be said. A bundle is represented in *fig. 4*. The elements which compose it are but two, spiraled ducts and tracheids with a peculiar flattened spiral, the latter being by far the more abundant. These alternate in time of development, showing what appear to be periodic changes. The very earliest portions of the xylem are composed of the ordinary spiraled ducts, irregular in size and position, and thereafter a small layer of these cells appears at what is probably the beginning of each season's growth. The flat spiraled tracheids, an element already mentioned by Ganong and Schumann, form in definite rows, each apparently the product of a single cambium cell, which, after cutting off the few irregular segments to form the spiraled ducts, apparently undergoes no more division by radial walls during the season. All the broadening of the bundles, therefore, occurs at the beginning of a period of growth. Likewise, when a branching is to occur, the resulting medullary ray appears at the beginning of the season, as shown in the drawing.

It seems likely that the flattening of the spiral in the tracheids, which compose most of the xylem, is what gives the elasticity so prominent in this bundle. Such a flattening inwards would allow a far greater stretching of the spiral than would be possible in the commoner round type. A fact which strengthens this assumption is that the walls of the tracheids in a preparation will be seen to be wrinkled between the spirals (*fig. 5*). In the living condition those were in all probability perfectly straight, and the turns of the spiral at a greater distance apart.

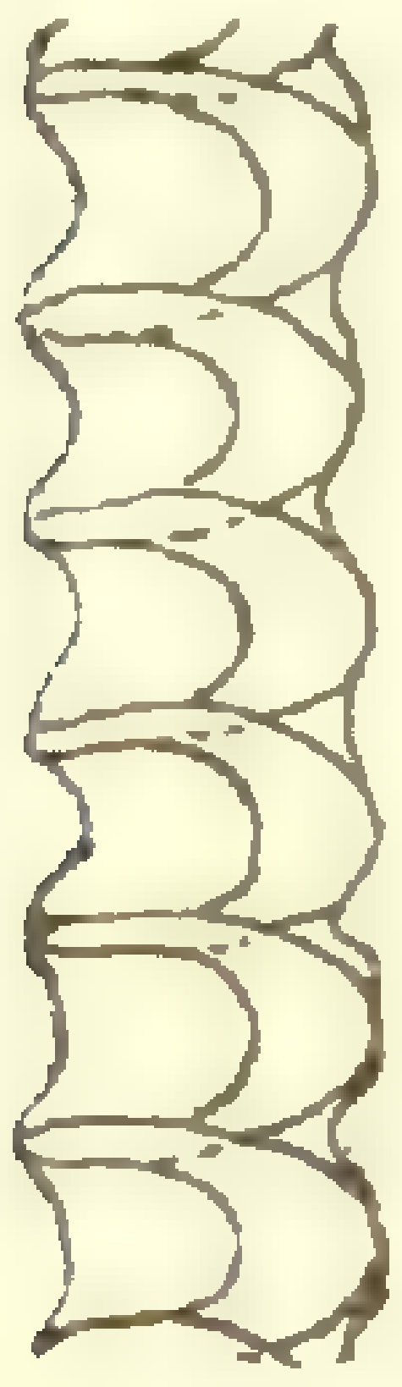


FIG. 5.—Portion of tracheid of flattened spiral type from xylem of stem bundle in *Cereus Fendleri.*

Another point which can be deduced safely from an examination of the figure is with respect to periodicity of growth. From the comparison with the amounts of earlier years, it will be seen that the xylem for the season was about half formed at the time of collection of material. As this took place in the latter part of December, it seems probable that the season of growth in the southwest is limited by the summer drouth and intense heat, rather than by the winter cold.

The branching of bundles and formation of secondary medullary rays in the stem is not of common occurrence in the Cactaceae, so far as my investigation goes. In most of the forms to be described a different state of affairs will be noted. The bundles of the root, however, branch in the ordinary manner in all the species I have examined.

The absorptive root[4] of *Cereus Fendleri* has a cork four to six cell layers in thickness. Successive layers of this kind are formed, with parenchymatous intervals, so that the bark is being constantly shed in flaky fragments, and is with equal rapidity replaced. The cork cambium lies a short distance outside the secondary phloem of the bundles. This phloem is composed almost wholly of sieve tubes which, when examined January 1, had no callus visible. Lateral plates occur in abundance, in addition to those at the ends of the cells.

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[4] BOT. GAZ. **30**: 348. 1900.

The xylem has but two elements, at least in the secondary portions. The more prominent, and by far the more abundant of these, is the tracheid, with ellipsoidal pits in more or less regular lines, an element which, from the shape of the pits, hardly coincides with the ordinary scalariform vessel, as seen in Pteris, for instance, but which, for convenience, I shall here designate by that term. Though the separate cells are comparatively short, there is often a continuous passage through several (a transition stage toward the true trachea), the walls between the adjacent cells being partially dissolved, and represented by nothing more than a thick and distinct ring. The other element is the obliquely pitted fiber tracheid, which apparently supplants the ordinary wood fiber in the majority of the Cactaceae.[5] The medullary tissue is but little compressed in the rays, giving a rather loose structure to the root as a whole. Crystals here, as also throughout the entire plant, are very few in comparison to their number in all the other species examined, occurring in the various parts of the parenchyma tissue, always in the aggregate form.

The anchoring root differs from the absorptive chiefly in the relative numbers of fibrous and vascular elements, as stated in a previous paper,[6] in which the phrase "wood cells" was used by mistake for "fiber tracheids." There is also a slight difference in the amount of sieve tissue developed in the phloem, the greater amount belonging naturally to the absorptive root. In species where the two systems are not clearly differentiated, the elements are more nearly equal as regards amount of space occupied by each. As a rule, the only difference between the two roots is one of proportion of elements, not of their variety.

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[5] For a drawing of this element see Strasburger's *Text-book of Botany*, translated by Porter, *fig. 143 ft.*

[6] BOT. GAZ. **30**: 348. 1900.

The absorptive root, therefore, will be the only one taken under consideration in discussing the remaining forms, except in one or two special cases. The difference between the two is hardly as well marked in *Cereus Fendleri* as in *Opuntia fulgida*, to be mentioned later.

ECHINOCACTUS WISLIZENI Engelm.—The epidermis and hypoderma are without crystals, the latter of six or seven layers of cells. The assimilative tissue is compact, with cells much elongated perpendicular to the surface, even in the sinuses between the ridges. The young parts do not develop chlorophyll in the sinuses until the ridges of tubercles, at first close-pressed together, become separated. The chlorophyll in this form is confined to a definite rind of palisade-like cells, which on the inside changes somewhat abruptly to a colorless parenchyma, rather thick-walled and fitted with a splendid system of pits and openings. Within this tissue are occasional crystals. Mucilage does not seem to be abundant in this species, but its place is taken by a watery solution, especially prominent in parts still growing, which upon long exposure to the air causes the tissue to assume a pinkish tinge. The medullary tissue about the bundles contains a fairly large quantity of starch, greatest in amount and widest in distribution in the young portions.

The bundles, as seen in cross section in a young stage, are not in a perfect circle, but rather in a zigzag line (*fig. 6*, diagram), with alternate points and depressions. There seems to be no branching or secondary medullary ray formation, and but little increase in the width of the original bundles. The zigzag line does not appear to be entirely the result of bundles passing out of the tubercles, for nearly all of the bundles in section appear to be cut directly across when all are cut in the same plane. They anastomose to a considerable extent, and, taking as centers the bundle at the base of each inner depression, join together with it to form a complex wood structure. The direction of growth of the side bundles is slightly inclined toward the central one, bringing the xylem of the whole group into close contact at an early stage. The phloem portions, however, remain distinct for each bundle. By this slight divergence, considerable medullary connection is left between the pith and the thick layer of storage tissue outside the poorly developed bundle cylinder, a far greater connection than could occur with the usual distribution, thickening, and branching of bundles seen in dicotyledonous stems. This peculiar grouping will be noted in a far greater degree of perfection in *Cereus giganteus*, next to be described. Here, as there, there seems to be no anastomosis of these groups of bundles, the incipient wooden ribs. In Opuntia, on the contrary, where this anastomosis of bundles likewise occurs to some degree, a still further reticulation is found, in that the groups as units anastomose.

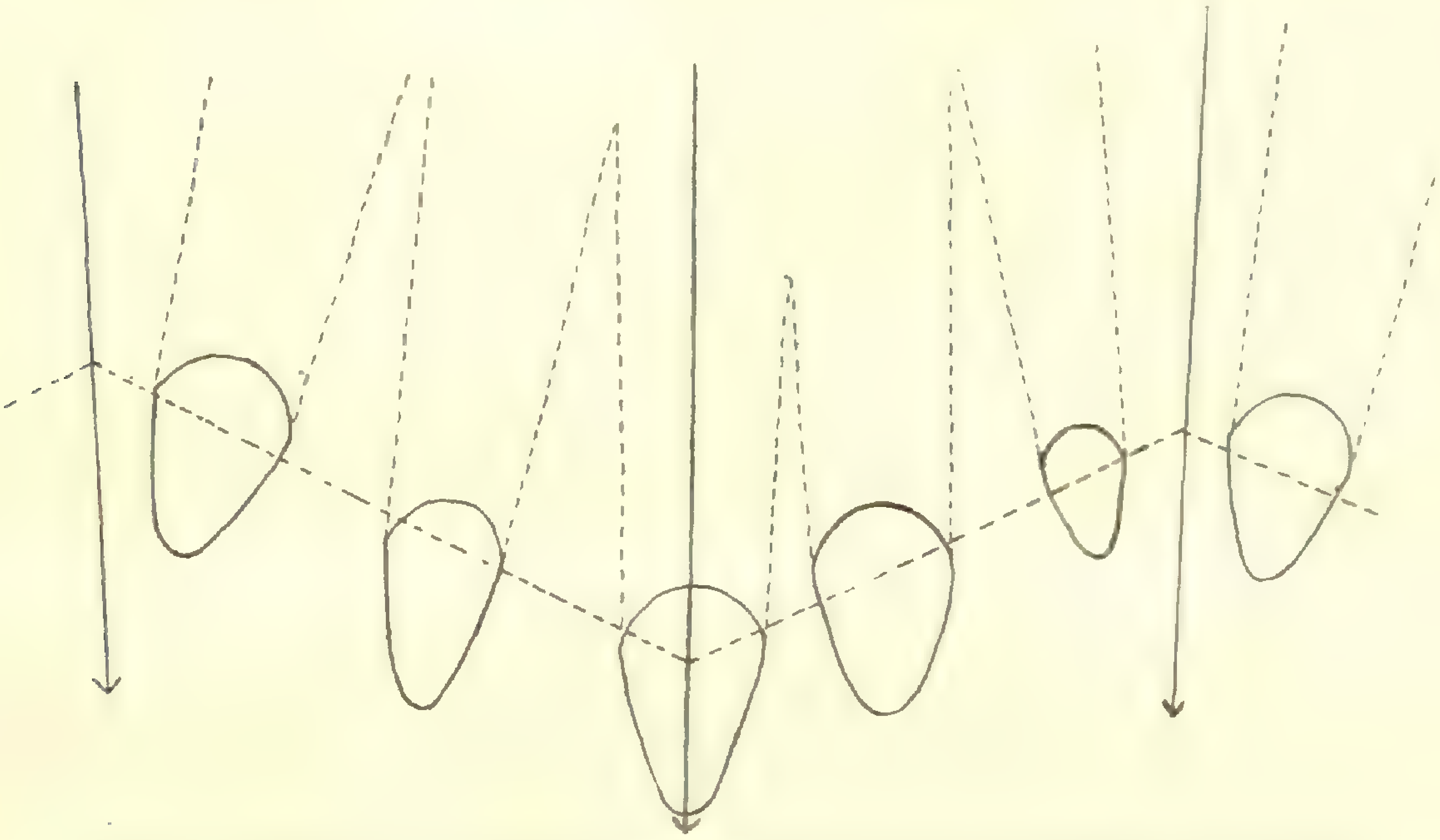


FIG. 6.—Diagram of position of bundles in *Echinocactus Wislizeni* and others.

As regards more minute structure in *E. Wislizeni*, the phloem is composed mainly of sieve vessels, the outer of which, together with the adjacent parenchyma, are composed and rendered sclerenchymatous, forming a sheath, here separate for each individual bundle. The xylem, at least in later portions, is composed entirely of spiraled tracheids of uniform size, but not in definite rows, the spiral also being of the ordinary type. A certain amount of elasticity of bundle occurs here, but nothing like that in *C. Fendleri.* The enormous amount of thick-walled parenchymatous storage tissues seems to have more effect in giving firmness to the internal structure than does turgor. The bundles have almost no supporting function, and are never well developed, appearing, in the widest part of a fair sized specimen, only 1^{cm} in thickness of xylem. The branches passing out to the tubercles or ridges divide through the tissues as in *C. Fendleri.*

The absorptive root contains numerous small crystals in the rays, more in proportion than appear in the stem. The chief xylem element is the scalariform tracheid; fiber tracheids also occur. In the anchoring root, as before, the proportions are reversed. The phloem is mainly composed of sieve tubes, but has a slight sclerenchymatous compressed sheath, a character which will be noted as fairly constant in both stem and root through the majority of forms.

CEREUS GIGANTEUS Engelm.—The epidermis and hypoderma are both without crystals, the latter being exceedingly thick, of twelve to fourteen layers of cells. The assimilative tissue is of the usual elongated cells, the filamentous arrangement of which is extremely well marked, to such a degree even that the filaments in a preparation can be separated easily. Chlorophyll extends deep into the tissue, and the elongated character of cell is found for nearly 20^{mm}. The medullary tissue is thick-walled and pitted, containing starch in the immediate vicinity of the bundles. Mucilage, though present in quantity sufficient to hinder the staining of sections, is not very thick. There is, however, especially in the younger parts, a watery solution apparently identical with that seen in *E. Wislizeni*, but much stronger, causing the tissue upon exposure to turn almost immediately from white to pinkish, and then to a dark purple.

In bundle formation, the method described for *E. Wislizeni* above is carried to greater perfection. Here not only do the bundles join their xylem portions, but all those of a single rib are surrounded by one sheath, formed gradually. In a young stage it may be seen outside each separate bundle, later two or more bundles are embraced by a single sheath, and this process apparently continues until all the bundles of the rib are thus bound together. This sheath is not the ordinary one of compressed sclerenchyma so commonly found next the sieve tubes. This outer one seems to be a special structure, composed of the obliquely pitted fiber tracheid so often mentioned, which here inclines more than ordinarily to the tracheid form, with wide lumen and with the extremities of the cells scarcely pointed. The individual cells are much larger than those of the same nature found in the xylem. The ribs alternate with the ridges of tubercles, both undergoing more or less branching. A full-grown rib, according to measurements taken from dead skeletons, seldom exceeds 3^{cm} in thickness. The phloem has the usual development of sieve tubes; the xylem is made up almost wholly of scalariform tracheids, an element so far noted only in the root. Besides these, there also occur fiber tracheids, undoubtedly in increasing proportion as the size of the rib and the corresponding function as a support increases.

The absorptive root differs from the others described in having in the phloem an abundance of fiber tracheids, forming a wedge pointing outward, starting just outside the sieve tubes of each bundle. These cells are also numerous in the xylem, together with the scalariform tracheids. Crystals are common in the cortex as well as in that of the stem, and are large and closely aggregate. They do not seem to be entirely homogeneous, but take some foreign substance as a nucleus. At times they appear to grow by concretion, showing when viewed in optical section a series of concentric circles.

The necessity for a fibrous strengthening in the absorptive root of this large form can best be understood by examining the method of growth. In starting as a seedling, the plant begins life with a base slightly sunken in the ground, but far narrower than the heavy column which it is to support. Therefore, as this column develops, the whole becomes very top-heavy, and would certainly fall were slightly greater surface exposed to the wind. The anchoring root, at this time well developed, holds it firmly to the ground, but only to a slight degree prevents a swaying movement, easily induced, even in plants 1.5^{m} high, by comparatively little force. Hence to the large lateral roots, developed from the sunken base at a later period, is given the function of steadying the whole plant, in addition to their primary work of absorption.

MAMILLARIA GRAHAMI Engelm.—The epidermis is free from crystals, but the one-layered hypoderma contains them in almost all its cells. The assimilative tissue is of small cells elongated, as usual, perpendicular to the surface. The colorless medullary portion is of thick-walled cells pitted as in *E. Wislizeni* and *C. giganteus*, and grades into the assimilative tissue. The lateral bundles can here be traced out into the tubercles. The stem bundles appear to start in a more or less wavy line, and to suffer fusion to some extent. There is comparatively little branching, but secondary medullary rays are occasionally found, and there is also a growth of the bundles in width, so that finally a rather compact cylinder is formed. As regards branching and internal structure of bundle, this species approaches *C. Fendleri* nearer than any of the others. The xylem is composed of alternating portions of spiraled ducts and tracheids of the flattened-spiral type, the latter being the more prominent. The phloem has a slight compressed sheath of sclerenchyma. Sieve tubes appear rather poorly developed, a thick-walled, somewhat elongated parenchyma taking up most of the region of the phloem.

In this small species there is apparently no distinction of anchoring and absorptive root systems. The bundle cylinder is compact, the pith practically absent, and the medullary rays reduced generally to a single cell layer. The phloem is slight and of sieve tubes. Outside the phloem, filling the small space between it and the cork cambium, is a parenchyma tissue of large rather thick-walled cells. The xylem consists chiefly of spiraled tracheids, with some amount of extra reticulation, and of smaller ringed ducts, the rings flattened inward, sometimes also bound together by extra spirals or reticulations. Crystals occur but seldom in the root, but are present in some quantity in the cortex and medulla of the stem.

Opuntia phaeacantha Engelm.—The hypoderma is rather thick, of six to eight layers, the outer one compactly filled with crystals, which occur also in great numbers throughout the assimilative and medullary tissues, clustering more or less about the bundles, but especially prominent in and about large duct-like spaces just exterior to certain of the bundles in both stem and root (Schumann's *Krystalschläuche*). Mucilage is fairly abundant. The assimilative cells are somewhat elongated, perhaps less so than in other forms so far recorded. Chlorophyll is deepest in the outer layers, but present as well in almost all parts of the deeper thin-walled parenchyma. The stem bundles form a loose reticulated network, branching early, especially on the flat surfaces of the stem, forming very wide secondary medullary rays. The phloem has the usual development with a sclerenchyma sheath. The xylem in early parts consists almost entirely of smaller annular ducts with flattened rings, but later forms spiraled tracheids and a large amount of obliquely pitted fiber tracheids.

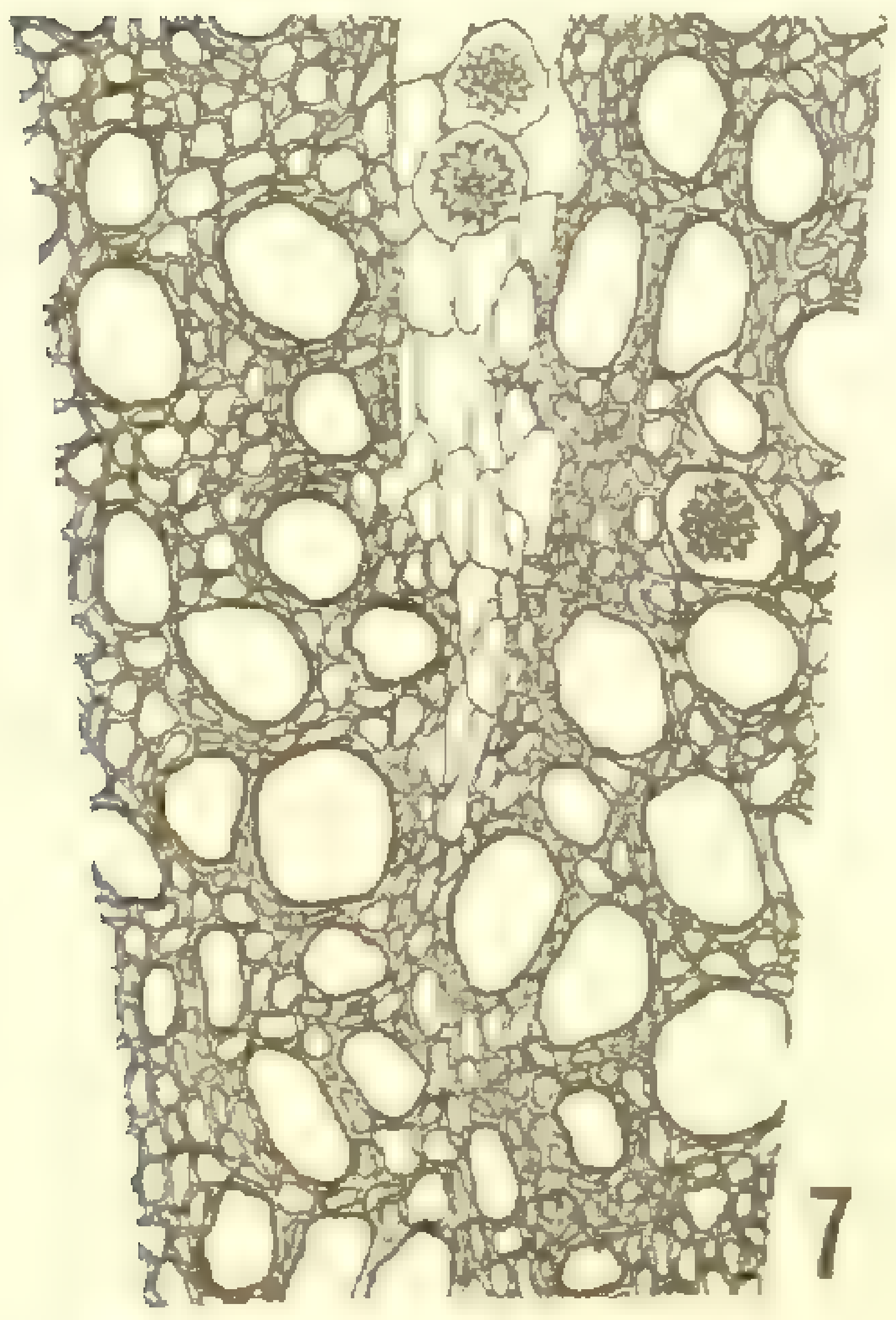
In the root especially are seen the *Krystalschläuche* in a high state of development, with a diameter of almost 1^{mm}. The crystals seem to be deposited mainly along the edges of the duct, which may serve also to some extent for the transfer of mucilage. The phloem of the bundle has a slight sheath; the xylem is composed of large and small scalariform tracheids and the usual fiber tracheids.

Opuntia fulgida Engelm.—The epidermis contains a deposit of crystals, a small quantity of which also occurs in the relatively thin hypoderma. The assimilative tissue is of cylindrical cells in lines, grading in the interior into large thin-walled parenchyma, also chlorophyllous. Mucilage is exceedingly abundant, and the ducts for its accommodation and transfer are both large and numerous. Large crystals, loosely aggregated, occur in small numbers throughout the tissue.

The bundles here remain very small through several joints,

Mo.Bot. Garden,
1902.

later becoming fused into a reticulated skeleton, the separate bundles of a single strand also anastomosing. The wavy line formation is seen to a slight extent in these Cylindropuntias also; there is apparently no branching, and little increase in width of bundle. The phloem presents no unusual characters; the xylem is composed of annular ducts, with flat rings at regular intervals; later on there occur also spiral tracheids, with steps grading to the true trachea.



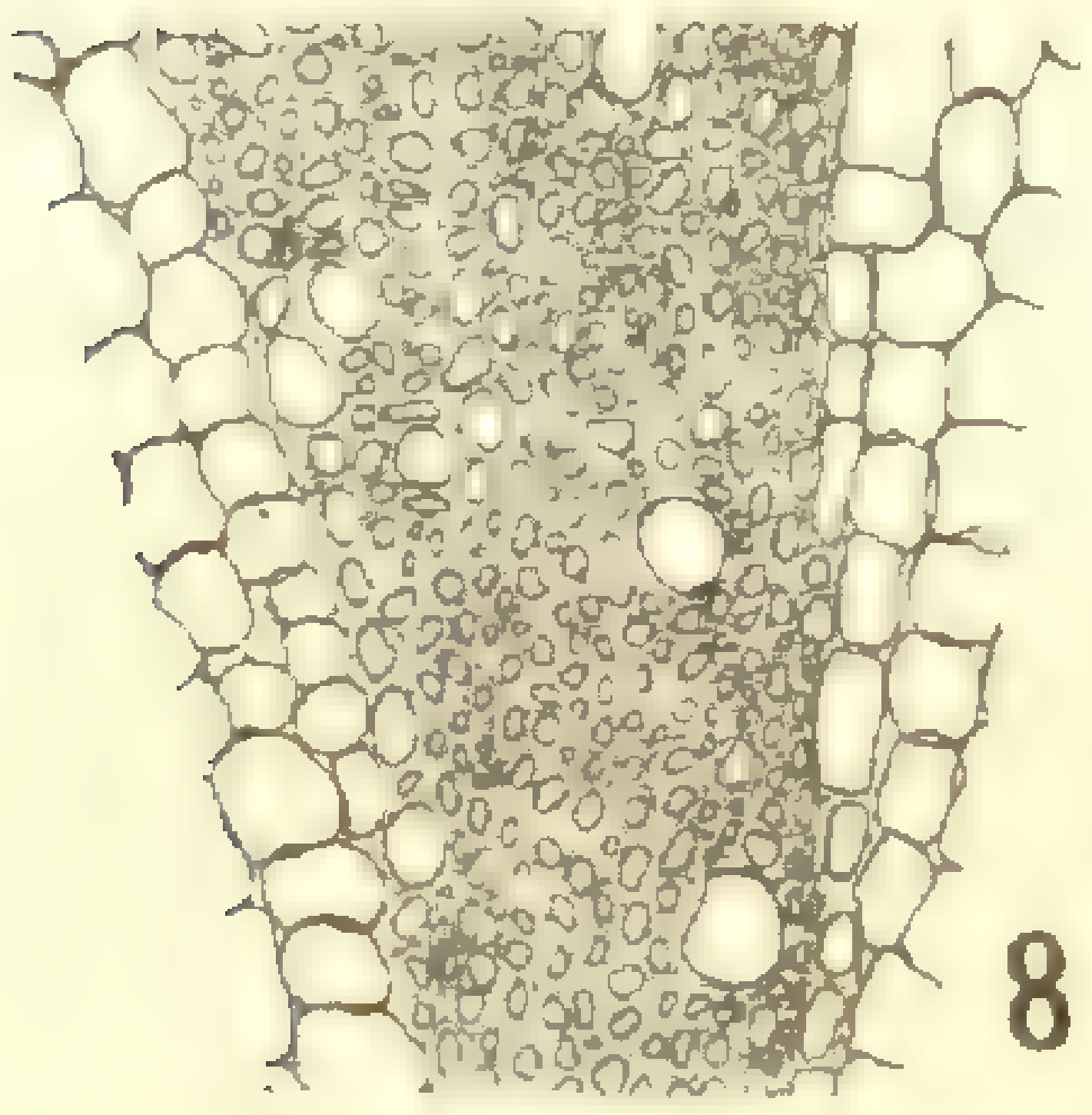


FIG. 7.—Cross section of portion of xylem from absorptive root of *Opuntia fulgida.*

FIG. 8.—Cross section of portion of xylem from anchoring root of *Opuntia fulgida.*

In an earlier article the roots of this species have been referred to as anchoring and absorptive. Portions of the xylem of each are figured here to show the difference in texture (*figs. 7, 8*). In the absorptive roots the elements are wider, more regular, and less thickened. The phloem differs but slightly in the extent of development of sieve tubes; the xylem differs as usual in proportions of elements, consisting in both of scalariform tracheids and fiber tracheids. From the prominence of the latter, both here and elsewhere, it would appear that the main function, if not the only one, which this element performs in the Cactaceae is one of support.

OPUNTIA ARBUSCULA Engelm.—The hypoderma is fairly thick, with a compact deposit of crystals in the outermost layer. The assimilative tissue is compact, the cells being small and greatly elongated in regions near the surface. The chlorophyll extends through the thin-walled parenchyma as well. Crystals are very abundant throughout, varying considerably in size and compactness of aggregation. The stem is very turgid and mucilaginous, kept rigid by turgor for some time, with late bundle development. The bundles finally form the same kind of reticulated skeleton seen in *O. fulgida.* The phloem is as usual; the xylem shows an occasional ringed duct, apparently an early element, but is principally composed of scalariform and fiber tracheids. Starch is present in considerable quantity through the stem.

The cortical parenchyma of the absorptive root is thickened in many places for storage purposes. The cells are filled with a thick mucilage, which aids in holding the water. A considerable deposit of starch, as well as of the regular calcium oxalate crystals, occurs in the medullary rays, but not at all in the cortex, an apparent differentiation of regions for various reserve substances. The phloem is of ordinary character, with a slightly developed sheath; the xylem is composed mainly of scalariform tracheids of various sizes, but contains a few fiber tracheids as well. A rather peculiar phenomenon is presented by the convergence of the cortical tissue toward the center of the phloem. Whether this was to hasten transfer of materials between cortex and phloem in young stages, before the sheath was thickened, in a way analogous to the clustering of palisade about the leaf bundles, which so commonly occurs, is a question which at once suggests itself, but upon which I am able to throw no light at present (*fig. 9*).

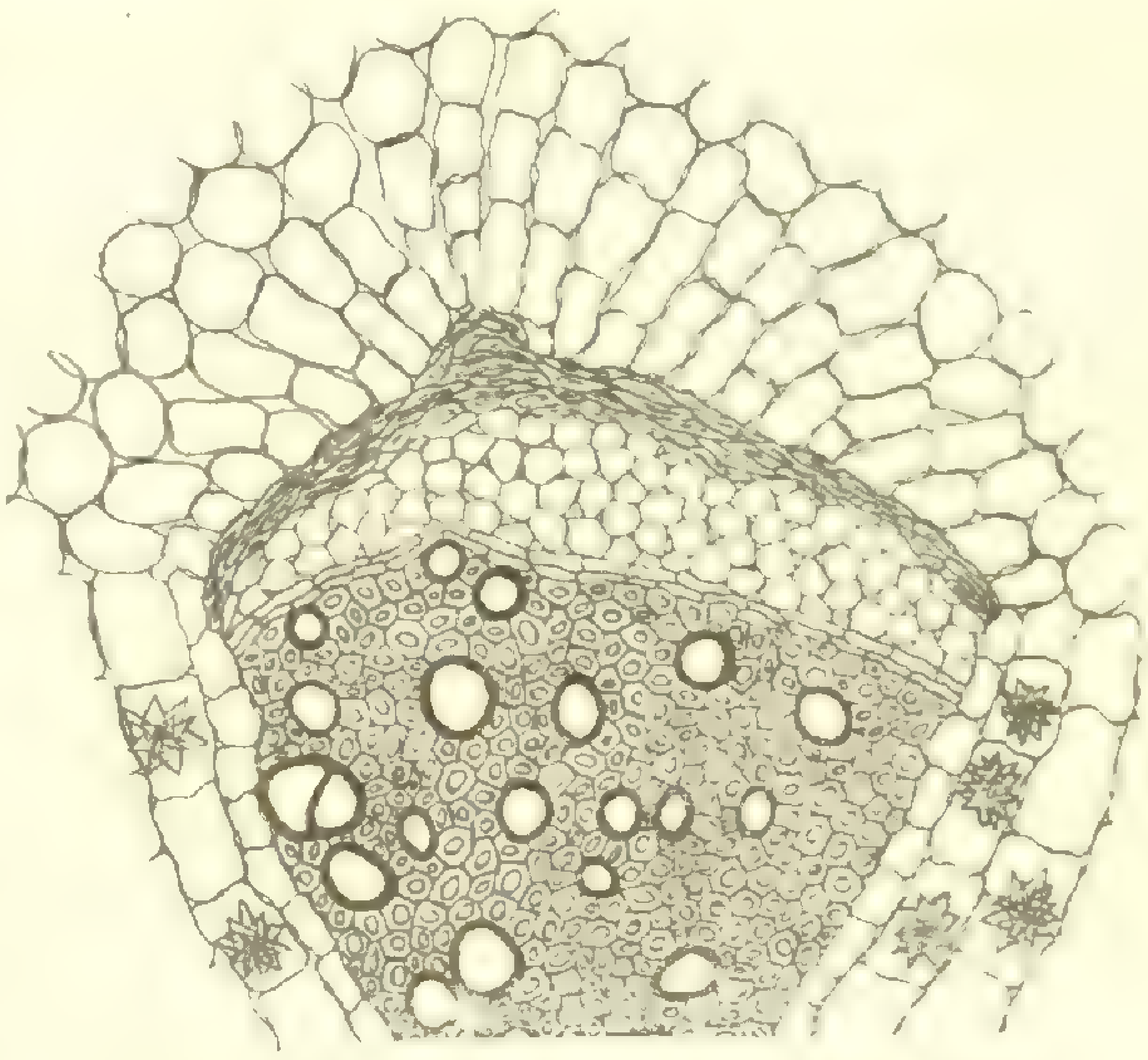


FIG. 9.—Portion of bundle from root of *Opuntia arbuscula*.

OPUNTIA LEPTOCAULIS DC.—The epidermis contains crystals in cells specially enlarged to receive them. The hypoderma is of four or five layers, and the assimilative tissue is elongated very slightly. The parenchyma of pith and cortex is nearly colorless, thin-walled, and contains considerable starch, evidently of the translocation variety. This species is not so succulent as the majority, and has an earlier development of the bundles. A point in which it differs from all the rest examined is in its possession of a well-marked interfascicular cambium in the stem, allowing the medullary tissue to increase in proportion to the growth of the bundle, instead of having the bundle compress and supersede it, as is apparently the condition in the others. That even here this cambium is not so active as that of the bundle seems to be demonstrated by the fact that outside the phloem the sclerenchyma sheath still appears compressed, though to a less degree. The xylem is composed mainly of fiber tracheids, intermingled with which are scattering spiraled ducts. The ordinary Opuntia reticulation occurs together with the finer anastomosis of the bundles of a single strand. Between these closely connected unbranched bundles the medullary rays develop very thick walls, apparently lignified, and are so filled with a deposit of starch that in section they appear much more opaque than does the rather close-grained wood on each side of them. Mucilage occurs, but not so abundantly as in the majority of cases, and crystals of rather small size are scattered through all the parenchyma tissue.

The root does not materially differ from those already described. The cortical parenchyma is slightly thickened, and the xylem is composed of the scalariform and fibrous types of tracheids.

SUMMARY AND CONCLUSION.—Several inferences may be drawn from the foregoing descriptions. In the first place, it will be seen that the roots, as regards branching and elements concerned, apparently undergo but slight variation, being composed, in almost all cases, of fiber tracheids and scalariform tracheids in the xylem, and of sieve tubes only in the phloem. To this general rule, as regards xylem portions, *Mamillaria Grahami* is the only exception among the forms here compared, and even in this the tracheid appears in greater prominence than the true duct. This exception, however, is enough to suggest that a more comprehensive examination will reveal more of a similar nature, and also perhaps disclose some links in the evolutionary chain between this and and the ordinary type.

In the stem, on the other hand, there is a great range of structural deviations, which seem to take place along definite lines and by definite steps. This variation extends to bundle branching and further reticulation, to the extent of succulence, character of parenchyma of pith and cortex, development of mucilage, and even to the kinds of elements composing the xylem of the bundle. In the phloem alone there is little change. The practically universal substitution of fiber tracheids for wood fibers, and the equally common appearance of tracheid elements in place of true ducts, except in early growth, points certainly to a general regression. The fiber tracheid, moreover, is variable in itself. In most cases it is quite sharply pointed and thick-walled, with a lumen, though broader than that of an ordinary wood fiber, still rather narrow. In a few instances, however, this same element loses its pointed character, widens its lumen still more, and except for its thick walls and oblique pits, scattered and exceedingly small, closely resembles an ordinary tracheid. This is very well shown in *Cereus giganteus*, a rather anomalous example, however, since here the fiber tracheid supplants a bast fiber instead of a wood fiber, and does not undergo an equal enlargement in the xylem portions of the bundle.

Crystal distribution and various storage peculiarities should be looked upon more as specific differences, I believe; likewise the thickness of hypoderma.

A word or two may be said of *Opuntia leptocaulis*. The early development of the bundles, the smaller degree of succulence, the persistent character of the leaves, at least in some varieties, as noted by Coulter,[7] the very slight elongation of the assimilative tissue, and above all the persistence of the interfascicular cambium, all tend to place this form in structure much nearer the ordinary dicotyledonous stem than any of the others examined. It seems safe to conclude that this species comes lower in the evolutionary line of adaptive modification than the rest of the Opuntias here mentioned, and may be considered nearer the primitive form.

[7] Contrib. U. S. Nat. Herb. 3 : 456.

Perhaps the most striking results of any to be found here from the systematic point of view will be obtained by a comparison of the first three forms. *Cereus Fendleri* and *Echinocactus Wislizeni* are entirely dissimilar as regards character of medullary tissue, mucilaginous contents, firmness of interior structure, and especially in respect to arrangement and branching of bundles. The third form, *Cereus giganteus*, corresponds in all the above mentioned peculiarities, not with the other Cereus, as would be expected, but with the Echinocactus. So far as I can tell from plates,[8] this closer resemblance to Echinocactus is carried out equally well in external characters, especially in those of the fruit, but to some degree at least in those of the spines and areolae (the last comparisons taken from living material). I have too little systematic knowledge of this group to contest the position of the species in classification, and can simply point to the fact that the two Cerei here mentioned belong at least to two different evolutionary branches within the genus, from one of which branches Echinocactus seems to have sprung.

The genus Cereus seems to me an especially fruitful field for the study of internal anatomy on a comparative basis. It is rather evident, from a hasty glance at the great variety of forms, that many different lines of development begin in this vicinity, lines which, though at present somewhat unraveled from external character, could at least be well subjected to confirmatory tests upon structural grounds. This would be of especial value in searching for the origin of the various other genera, the supposed offspring of this group.

It must not be thought, however, that I wish to give too great importance in classification to the internal anatomy, preferring it to the external characters. Its principal use is confirmatory. Too many internal variations spring up independently in several forms to make them alone sufficiently reliable. There must be some gradual internal metamorphosis, however, to correspond with the external. In what deep-seated organs this is shown, and what parts are more easily influenced by environmental conditions, can best be determined by careful study. At present I am inclined to believe that the most permanent and satisfactory evolutionary characters will be found in the fibrovascular system. When its metamorphosis is fully understood a far clearer insight can be gained, not only into the interrelationships of these peculiar and at present much confused groups of plants, but also into the steps by which they became gradually accustomed to their present rigorous habitat.

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[8] Engelmann's Cact. Mex. Boundary.

Harvard University.

Later investigation shows that the statement (p. 42, line 17 ff.) regarding periodicity of growth is incorrect. The smaller amount of growth noted was due to the drouth of the summer of 1900. In spite of their storage facilities, these plants are apparently affected by temporary unfavorable conditions to a degree almost surprising.

BRIEFER ARTICLES.

NOTE ON BASILIMA AND SCHIZONOTUS OF RAFINESQUE.

As *Basilima* of Rafinesque is still considered by many botanists to be the valid generic name for the genus based on *Spiraea sorbifolia* Linn., it will probably not be uninteresting to point out that it has no claim to the priority attributed to it. Until 1891 the genus has been best known under the name Sorbaria, proposed first by Séringe (DC. Prodr. **2** : 545. 1825) as a section of Spiraea, and given generic rank by A. Braun (Ascherson's Flor. Brandenb. 177. 1864). In 1891, however, E. L. Greene (Flor. Francisc. 57) and O. Kuntze (Rev. Gen. Plant. **1** : 215) almost simultaneously took up the Rafinesquean name Basilima for Sorbaria, and claimed priority for it on the ground that Rafinesque in his *New Flora of North America* (3 : 75. 1836) quotes "Raf. 1815" as authority for his Basilima, but neither of them seems to have seen or even known the original place of publication. If they had seen it, they would have been aware that Basilima of 1815 is a *nomen nudum* pure and simple, and therefore not entitled to priority. Rafinesque unfortunately makes no mention of the place of publication, but after some searching I was fortunate enough to find the name in his *Analyse de la nature ou tableau de l'universe et des corps organisés*, a very rare book of 244 duodecimo pages, published in Palermo in 1815. It aims to give a short review of the whole range of natural history, and contains on page 173, under the order Rhodanthia, the following passage reproduced here verbatim et literatim :

> 5. Famille Spireadia. Les Spiréades. Etamines hèterines, perigone double, l'interne corollé, fruits capsules dehiscentes interieurement. G. 1. Spirea L. 2. Rhodalix R. sp. do. 3. Drymopogon R. sp. do. 4. Basilima R. sp. do. 5. Filipendula T. 6. Gillenia Mench.

From this enumeration it is impossible to gain any idea which species of Spiraea Rafinesque intended to include under his genera Rhodalix, Drymopogon, and Basilima, and he could therefore not claim priority for it, as he does, and quote as synonyms of his Basilima two names published before 1836. The older of these two names is the Sorbaria of Séringe mentioned above, the second the Schizonotus of Lindley, published in 1830 in his *Introd. Nat. Syst. Bot.*, p. 81, and (under no. 703) in Wallich's *Catalogue*, which appeared about the same time. In both places, however, the name is mentioned only as a synonym, and it seems doubtful whether this ought to be considered as a real publication of a generic name. The passages in both publications read as follows: Wallich, Cat., p. 21, "no. 703. Spiraea Lindleyana Wall. Schizonotus Lindl. (gen. nov. Spir. sorbifoliam amplectens);" Lindl. Introd. Nat. Syst. Bot. ed. 1, p. 51, "Rosaceae. . . . . The fruit of Spiraea sorbifolia (Schizonotus m.) is capsular." In the second edition of his work, however, which appeared in 1836, Lindley enumerates (p. 145) Schizonotus as a genus, and characterizes it (p. 441) by mentioning *Spiraea sorbifolia* as the type. In the same year, Rafinesque published in *New Flor. N. Am.* (**3**: 75-76) the genus Basilima, with descriptions of two species, *B. sorbifolia* and *B. pygmaea.* As it seems impossible to ascertain which of the two works was really published first, the genus Basilima ought to be preferred, since it had specific names attached to it, while Schizonotus had none and received none until 1840, when Lindley (Bot. Reg. **26**: misc. 71) proposed the name *Schizonotus tomentosus* for *Spiraea Lindleyana* Wall.

Those botanists who object to Sorbaria because it was published only as a sectional name must therefore choose between Schizonotus and Basilima. It would be very unfortunate, however, to revive the name Schizonotus, since it was applied afterwards and has been in use for two other genera, first to a genus with *Spiraea discolor* Pursh as the type by Rafinesque, who entirely misunderstood a note of Lindley in *Bot. Reg.* **16**. 1830 in the text to *pl. 1365*, and says in *New Flor. N. Am.* **3**: 75 under Schizonotus "I have adopted this genus and name on the suggestion of Lindley, who proposed to unite to it the next [Basilima], but the habit is too different." But Lindley did not say this. He only mentions there on the same page these two species of Spiraea, together with some others, and the name Schizonotus. The second application of the name Schizonotus was by A. Gray (Proc. Amer. Acad. **12**: 66. 1876) to a genus of Asclepiadaceae, which was subsequently changed by E. L. Greene to *Solanoa;* while on *Spiraea discolor* the name *Holodiscus* was bestowed first by C. Koch, who proposed it in his *Dendrologie* (**1**: 309. 1869) as a subgenus of Spiraea, which was afterwards given generic rank by Maximowicz in his excellent monograph of the Spiraeaceae (Acta Hort. Petr. **6**: 253. 1879).

without either of the authors being aware of the existence of a *Schizonotus* Raf.

In *Index Kewensis* the Schizonotus of Lindley and of Rafinesque are not discriminated, but wrongly united under *Schizonotus* Lindl.; while *Schizonotus* Gray is enumerated as valid. Also the *Thecanisia discolor* Raf. is there erroneously made a synonym of *Spiraea discolor*, but it is an herbaceous plant allied to *Ulmaria rubra*, and probably based on escaped plants of the European *U. pentapetala* Gilib. (*Spiraea Ulmaria* Linn.)

It will be clear that on account of priority as well as of usage the name Sorbaria ought to be considered as the valid name, with *Schizonotus* Lindl. (1830) and *Basilima* Raf. (1836) as synonyms; while *Holodiscus* (Koch) Maxim. should be substituted for *Schizonotus* Raf., at least by those who follow the Rochester rules in accordance with article IV, and by others on account of expediency, to avoid all possible confusion with the other two genera, of which one is liable to be revived under certain rules of nomenclature.

Sorbaria of course will not enter into the American flora if Chamaebatiaria is considered as constituting a distinct genus, which it may be, though structural differences in flower and fruit are hardly present. In foliage and habit, however, it is strikingly different. The observation of Rafinesque that *Sorbaria sorbifolia* is a native of Northwest America seems not to be based upon any reliable source, at least it has not been found again on American soil, neither has *S. grandiflora* Maxim. (*Basilima pygmaea* Raf.), which was suspected by him to occur probably somewhere in the same region.—ALFRED REHDER, *Arnold Arboretum.*

POTAMOGETON POLYGONIFOLIUS IN NEWFOUNDLAND.

THE only note of the occurrence of this species in North America I know of is contained in Linnaea **2**:216. 1827; where Chamisso has the following: "Hujus loci forsitan est: Potamogeton de St. Pierre Miquelon près Terreneuve in Herb. Brogniart, sed major." I have not seen the specimens in Brogniart's herbarium, which is at Paris.

In the *Journal of Botany* for June of this year, I record it from Sable island, about 100 miles off the coast of Nova Scotia. I have now to record it from Newfoundland, from whence I find specimens the Kew herbarium from the herbarium of Harvard University.

As this was gathered by American botanists I record it in an American journal, the more so as I wish to point out that there is some hope it may occur in Massachusetts in the neighborhood of where *Calluna vulgaris* L. occurs. The label of the Newfoundland specimens runs thus:

No. 231. *P. heterophyllus* Schreb. Muddy banks of brooks. Whitbourne. 17. 8. 1890. Coll. B. L. Robinson (and) H. Schrenk. Distributed from the Herbarium of Harvard University.

The two specimens are not *P. heterophyllus,* however, but *P. polygonifolius* in its usual "heath" form. As this is the first time it appears in American books it may be well to give the synonymy and distribution.

P. POLYGONIFOLIUS Pourr. in Acad. Toul. **3**:325. 1788.

P. oblongus Viv. Anal. Bot. **2**: 102. 1802; also in Fragm. Fl. It. **1**: 1. *pl. 2.* 1808.

P. plantago Batard, Fl. dep. Maine et Loire 64. 1809.

P. parnassifolius Schrad. (ined. 1818) ex Mert. et Koch, Deut. Fl. **1**: 839. 1823.

P. uliginosus et *affine* Boenning ex Cham. in Linnaea **2**: 216. 1827.

P. paludosus Bory in sched. ex Cham. *l. c.*

P. natans intermedius Mert. et Koch, Deut. Fl. *l. c.*

P. microcarpus Reut. et Boiss. Diag. Pl. Nov. Hisp. **2**:24. 1842 is a variety, or perhaps a subspecies.

DIST. EUROPE: Iceland to Piedmont, and Holland to Russia.

ASIA: Siberia altai (Led.) to Mongolia, and China to India and Japan.

AFRICA: Morocco to Transvaal? (Wilms), and Madagascar.

AUSTRALIA: New Zealand.

The species varies greatly, the var. γ *ericetorum* Syme, Eng. Bot. ed. 3, **9**: 28. 1869, representing the small heath form, often growing in mud, the var. β *pseudo fluitans* Syme, *l. c.*, the other extreme, *i. e.*, a fluitant form often in deep or running water with thin translucent submerged leaves and coriaceous upper leaves.

It may be distinguished from *natans* by the small fruit, the blunt stipules, the base of the leaves never having the flexible joint of *natans* (there are no "strings" in the leaf of *polygonifolius*) which enables that species to turn its leaves in any direction; from *heterophyllus* by the style being central, by the nervation of the leaves, etc.

I hope to send specimens of this species to various American botanists next fall, so that they may know it and keep it in view.—ARTHUR BENNETT, *Croydon, England.*

A NEW SPHAERALCEA.

Sphaeralcea martii, n. sp.—Perennial, low and rather spreading, 15 to 30^{cm} high: leaves and stems whitish-green with an excessively dense white stellate pubescence: leaves subhastate, with broad short basal lobes, crinkled, edges coarsely irregularly serrate, about 27^{mm} long and 15^{mm} wide; petioles about 10^{mm} long: flowers large, 23^{mm} in diameter, in clusters of six or seven at the ends of the branches; pedicels 5 to 7^{mm} long: calyx 11^{mm} to tip of lobes, 4^{mm} to base of lobes: petals fully 15^{mm} long and broad, rather pale but vivid scarlet (dull pink in dry material): anthers orange; pollen bright orange: styles crimson: fruit maliform, densely white-hairy; carpels with very small beaks; ovules two in a cell.

Picacho mountain, Mesilla valley, New Mexico, in volcanic soil, March 25, 1900 (*Cockerell*); hills north of Picacho mountain, April 7, 1900, in fruit (*E. O. Wooton*). A specimen is in Herb. U. S. National Museum.

Differs from *S. subhastata* in its pointed leaves, clustered flowers, deeply cleft calyx with long acuminate lobes, and especially in its early flowering, wherein it resembles the annual species. The only flowering date I find reported for *S. subhastata* is in August.—T. D. A. COCKERELL, *East Las Vegas, N. M.*

CURRENT LITERATURE.

BOOK REVIEWS.

Handbook of systematic botany.

THE first volume has appeared of a handbook on systematic botany by Dr. Richard R. v. Wettstein,[1] of the University of Vienna. We do not often have texts that confine themselves so closely and accurately to the subject as does this very excellent outline of classification. Its aim is to give a general view of the plant kingdom with especial reference to the evolution of phylogenetic lines. Prefacing the special parts, which deal specifically with the groups of plants, there is a general treatment of a number of interesting topics. There is first an historical account of the development of systematic botany, which one wishes were longer. This is followed by discussions of the conditions which lead to the development of lines (phyla) of ascent and the sort of evidence of value in the determination of the same. There is an excellent account of the methods of systematic botany and the data of most value in studies on classification. Admirable illustrations are presented of analogous and homologous organs, rudimentary structures and juvenile forms. Finally the author considers the origin of new forms on the supposition of phylogenetic evolution, or in other words the principles of Darwinism. This is in the main a simple account of evolutionary factors, and is particularly good in the treatment of adaptation and the changes in species effected directly by environment. At this point the author shows clearly the importance of the so-called ecological factors in the definition and adjustment of species.

Following the short general part, which is only forty-four pages long, comes the special part that will deal entirely with the various groups.

The present volume ends with the thallophytes, but we are promised the completion of the subject next year. The author divides the plant kingdom into seven branches, as follows: 1) Myxophyta, 2) Schizophyta, 3) Zygophyta, 4) Euthallophyta, 5) Phaeophyta, 6) Rhodophyta, and 7) Cormophyta. The success of a division into great groups depends primarily upon the balance maintained, and this one has some peculiar disadvantages in its lack of symmetry. It will hardly be questioned that branches 1, 2, 3, 5, and 6 are well differentiated phyla or closely related groups of phyla. But this simplicity is all out of proportion to the complex conditions presented in the

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[1] WETTSTEIN, RICHARD V.: Handbuch der systematischen Botanik. Vol. I. 8vo. pp. vi+201. *figs. 762.* Leipzig: Franz Deuticke. 1901.

Euthallophyta and Cormophyta. Passing to the detailed subdivision of the main groups, the descriptions of orders and families and the illustrations are generally very good. We note that the Protococcaceae and Hydrodictyaceae are placed at the bottom of the large order Siphoneae, a position that is certainly open to question. The Charales are reduced to a suborder of the same group, which seems curious for so highly specialized and well defined a line of development. Among the fungi the Brefeldian system is followed in part, with much of the arrangement in Engler and Prantl; and the classification of the Phaeophyta and Rhodophyta is a brief outline of the latter work. These two groups are not given the attention they deserve.—B. M. DAVIS.

MINOR NOTICES.

HERMANN VON SCHRENK has published[1] his address on "Factors which cause the decay of wood," delivered before the Western Society of Engineers on February 6 last. It deals with such topics as structure, chemical nature, and decay of wood, fungi and structural timbers, and preventive measures.—J. M. C.

THE THIRD FASCICLE[2] of the list of the genera of seed plants, according to the system of Engler, has just appeared. The general character of the work was stated in this journal[3] in the notice of the first part. In the present signature 1352 genera are listed, bringing the number up to 3842, the list beginning with Lychnis (Caryophyllaceae) and ending with Geoffraea (Leguminosae).—J. M. C.

F. LAMSON-SCRIBNER[4] has published a revised edition of the second part of his *American grasses*, the first edition having been exhausted. The work has been entirely rewritten, the synonymy has been revised or extended, and the descriptions are much fuller. The two parts now contain illustrations and descriptions of 627 species, and are invaluable to those who would name grasses.—J. M. C.

CHARLES V. PIPER and R. KENT BEATTIE[5] have published a manual of the flora within a radius of about twenty-one miles around Pullman, Wash. This includes some twenty-four townships in Washington and eleven in

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[1] Reprint from Jour. Western Soc. Engineers, May 1901.

[2] DALLA TORRE, C. G. DE, and HARMS, A.: Genera Siphonogamarum ad systema Englerianum conscripta. Fasciculus tertius (signatura 21–30). Small 4to. pp. 161–240. Leipzig: Wilhelm Engelmann. 1901. *M* 4.

[3] BOT. GAZ. 30:67. 1900.

[4] American grasses. II. Revised edition. 8vo. pp. 349. Bulletin 17, Division of Agrostology, U. S. Department of Agriculture. 1901.

[5] The flora of the Palouse region. 8vo. pp. viii + 208. Published by the Washington Agricultural College and School of Science, Pullman. May 14, 1901.

Idaho, the region consisting mainly of rolling hills, destitute of trees and shrubs, and said to be quite typical of a large area in eastern Washington and western Idaho. These hills are generally called Palouse hills, and hence the title of the book. The manual certainly covers a region of very great interest in its unrivaled floristic riches. The keys and descriptions seem to be entirely adequate, and, checked as they have been by the large field experience of the authors, the manual must give as good a presentation of the flora as is possible at present. The nomenclature follows what are called the Kew and Berlin rules. Several new species are described, and the enumeration of species shows 14 pteridophytes, 9 gymnosperms, 114 monocotyledons, and 526 dicotyledons. The exceedingly varied conditions of the western mountain region will demand the publication of just such local manuals as this.—J. M. C.

THE LIVERPOOL Marine Biological Committee is doing good work in publishing short popular papers on the more interesting animals and plants in the general region of its activities, the Irish sea. The first three papers described animals, but the fourth, just issued, is on Codium,[6] a very interesting genus of the Siphonales. Following a general introduction, we have presented an account of the structure, reproduction, habits, and distribution of this alga. The life history is still incomplete in certain phases of reproduction. There are two forms of sporangia, one producing large green zoospores and the other small yellow elements, both however morphologically similar and biciliate. The larger green zoospores will germinate vegetatively, and the problems concern the fate and function of the small yellow bodies. They have been supposed to be sperms that should fuse with the green swarmers, but no unions have ever been observed. It is probable that the yellow zoospores are gametes, which under suitable condition will conjugate with one another. The authors of the paper suggest that the plant is becoming apogamous, a view that has support, further than the mere negative evidence, in the fact that the hypothetical gametangia at certain stages in their development may be reproductive. They are then adventitious buds, capable of growing out in a branching filament, which however appears to remain attached to the parent plant. The paper is illustrated with three very clear plates.—B. M. DAVIS.

NOTES FOR STUDENTS.

THE POLLEN tube in *Cucurbita Pepo* according to B. Longo[7] traverses the tissues of the funiculus and outer integument before entering the micropyle. The writer proposes the name *mesogamy* for this phenomenon.—CHARLES J. CHAMBERLAIN.

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[6] GIBSON and AULD: Codium. pp. viii+18. *pls. 3*. L. M. B. C. Memoirs. IV. 1900.

[7] La mesogamia nella commune zucca (*Cucurbita Pepo* Linn.). Rendiconti della R. Accademia dei Lincei **10**: 168–172. 1901.

DR. N. WILLE[8] has begun a series of studies on the Chlorophyceae. The first paper contains numbers one to seven, and treats of the structure and phases in the life histories of *Sybidion Droebakense*, n. sp., Trochiscia, *Prasiola crispa*, *Ulothrix flacca* and several new species of Ulothrix, Pseudendoclonium, nov. gen., and certain species of Rhizoclonium. Four excellent plates accompany the text.—B. M. DAVIS.

AS A RESULT of experiments conducted in Maryland in the seasons of 1899 and 1900, C. O. Townsend finds[9] that celery blight, caused by the fungus *Cercospora apii*, can be prevented by the use of fungicides. The best results, apparently, are given by ammoniacal solution of copper carbonate, Bordeaux mixture being equally good as a fungicide but causing a slight stunting of the plants. To obtain the best results the first application should be made while the plants are still in the seed-bed, followed by other applications every week until cool weather, which checks the progress of the disease. —ERNST A. BESSEY.

THE SUBJECT of oat smut has received attention in two recent bulletins from the Illinois[10] and Wisconsin[11] experiment stations respectively. In both an estimate is given as to the annual loss in the state from this smut, about 14 per cent. for Illinois and about 6 per cent. for Wisconsin. The results of experiments with the hot water treatment at different temperatures are described in the former bulletin, the temperature found to be most efficient without injury to the germinative power of the grain being 135° F. for five minutes. Both bulletins discuss the formalin treatment, which is shown to be even more effective than that with hot water and somewhat more easy to perform. — ERNST A. BESSEY.

A SHORT NOTE on the abundant and destructive occurrence of the dwarf mistletoe, *Arceuthobium pusillum*, in the upper peninsula of Michigan is given in a recent bulletin from the Michigan Experiment Station.[12] In connection with the recent rediscovery of this interesting plant in New England, it is of interest to note that in Michigan it is in some places so abundant as to kill out nearly every tree. The parasite itself is attacked by a fungus, *Wallrothiella arceuthobii* Peck, which apparently serves to keep it in check somewhat. In the same bulletin are given notes on the trees and a list of the flowering plants growing on the station farm, as well as a list of the few of the commoner diseases of cultivated plants observed there.—ERNST A. BESSEY.

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[8] WILLE, Dr. N.: Studien über Chlorophyceen. Med. f. d. biol. sta. v. Dröbak. no. 2. 1901.

[9] TOWNSEND, C. O.: Notes on celery blight. Bull. Maryland Agr. Exp. Sta. no. 74. pp. 167–182. *figs. 1–7*. May 1901.

[10] SHAMEL, A. D.: Treatment of oats for smut. Bull. Ill. Agr. Exp. Sta. no. 64, pp. 57–72. *6 pls.* Urbana. March 1901.

[11] GOFF, E. S.: The prevention of oat smut. Special Bulletin, Wisconsin Agr. Exp. Sta. pp. 1–4. *fig. 1.* Madison. March 1901.

[12] WHEELER; C. F.: The geology and botany of the Upper Peninsula Experiment Station. Report of the Upper Peninsula Experiment Station for the year 1900. Bull. Michigan Agr. Exp. Sta. no. 186. pp. 17–28. *4 pls.* Dec. 1900.

D. T. MACDOUGAL[13] has studied the bulbils which are formed in the axils of the aerial stems of *Lysimachia terrestris*, and regards them as representing a new category of propagative bodies. They are branches of restricted development, and are formed under conditions unfavorable for seed formation, diffuse light and low temperature apparently being the principal inciting causes. They are free from transpiratory organs of any kind, and resemble rhizomes in structure rather than aerial stems upon which they are borne. The "germination" of the bulbil occurs without any appreciable resting period, and is followed by the final stages of the differentiation of the stele, which was checked during the formation of the bulbil. The bulbil becomes the main axis of the new plant, and does not perish, except gradually, after the manner of a rhizome, into which it becomes converted.—J. M. C.

MUSHROOMS ARE DISCUSSED in two recent Experiment Station bulletins, one from Idaho[14] and the other from North Carolina.[15] Both give rules for avoiding poisonous fungi and analyses showing the food value of the edible species. This has been greatly overrated, for, compared with other foods, these fungi have not only a small heating power but have also a low nitrogen content. In the former bulletin a few species are popularly described with the aid of good half-tone plates, while in the bulletin from North Carolina all or nearly all of the edible species reported in the state are described, rather too technically it would seem. This technicality, combined with the lack of illustrations, leads one to fear that it will not be serviceable as a popular guide. The glossary, five pages in length, is no doubt necessary but might have been made more accurate. The definition of basidia as "cellular processes of certain mushroom-bearing spores" is probably a typographical error, but is plainly very misleading as it stands.—ERNST A. BESSEY.

THE THIRD EDITION of Sturgis's *Literature of Plant Diseases*[16] brings the bibliography of these diseases nearly up to date. The first edition appeared in 1893 and the second in 1897. It does not assume to be a complete bibliography, but a reference list "to enable the practical observer of plant diseases to ascertain what are the principal sources of information regarding the specific cause of a certain disease and the method of prevention as recorded in the publications of our own Department of Agriculture and of the various state experiment stations." As in the previous editions, the host plants are arranged alphabetically under their common names. A number of diseases formerly ascribed to parasitic organisms but since shown to be due to other causes are omitted, while many new host plants whose diseases have been studied in this country only in recent years are added, making the list now somewhat longer than before. The work is exceedingly useful not only to the practical worker but also to the specialist.—ERNST A. BESSEY.

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[13] Propagation of *Lysimachia terrestris*. Bull. N. Y. Bot. Garden **2**: 82–89. 1901.

[14] HENDERSON, L. F.: Mushrooms or toadstools: a natural food product. Bull. Idaho Agr. Exp. Sta. no. 27. pp. 27–54. *figs. 1–12.* Moscow. March 1901.

[15] HYAMS, C. W.: Edible mushrooms of North Carolina. Bull. N. C. Agr. Exp. Sta. no. 177. pp. 25–58. West Raleigh. Dec. 1900.

[16] STURGIS, W. C., Literature of plant diseases. A provisional bibliography of the more important works published by the U. S. Department of Agriculture and the agricultural experiment stations of the United States from 1887 to 1900 inclusive, on fungous and bacterial diseases of economic plants. Rep. Conn. Agr. Exp. Sta. for year ending Oct. 31, 1900. Part III. pp. 255–297. 1901.

THE ZYGOSPORE OF SPORODINIA was studied six years ago by Léger, who found that both gametes contain hundreds of small nuclei which become scattered in the mingling cytoplasm when the membrane separating the gametes breaks down. The nuclei near the periphery are much smaller than those nearer the center. At a later stage all the nuclei disappear, and at each pole of the zygospore there is found an "embryonic sphere" containing a large number of granules. The spheres increase in size and fuse with each other, and soon afterward numerous nuclei again appear. Gruber[17] has examined Sporodinia, and he also finds a large number of nuclei in the zygospore. The nuclei are more numerous at the periphery, but those at the periphery and those at the center are approximately alike in size. This condition persists for a long time, and subsequent stages were hard to follow. No fusion, division, or disorganization of nuclei could be established with any certainty. The presence of "embryonic spheres" is regarded as doubtful. On germination the nuclei appear in greater numbers and pass into the germ tube. Although the writer was not able to observe any fusion of nuclei, he believes that a fusion of nuclei at the center of the zygospore is very probable. —CHARLES J. CHAMBERLAIN.

THE EFFECT of fungicides upon the foliage of the peach is discussed by W. C. Sturgis in a recent report of the Connecticut Agricultural Experiment Station.[18] The experiments were made with various strengths of Bordeaux mixture, with a soda-Bordeaux, in which soda replaced the lime, with ammoniacal solution of copper carbonate, with copper acetate, and with potassium sulfid. The Bordeaux mixture was found to be injurious to the foliage except when very weak solutions were used. The soda-Bordeaux was also injurious, as was the ammoniacal solution of copper carbonate. Potassium sulfid, however, proved to be harmless, and at the same time to be a fairly good fungicide. Normal copper acetate solution was harmless but the subacetate caused injury. Careful comparative examinations of leaves of plants susceptible to injury by copper-containing fungicides, viz., peach, Japanese plum, and apricot, with leaves of plants not so injured, viz., European plum, apple, cherry, quince, and pear, failed to reveal any constant difference in the thickness of the leaves as a whole, or of the epidermis and the different layers of tissue, or in the size or number of the stomata. The susceptible leaves, however, had a very dense spongy parenchyma, with small intercellular spaces, while the non-susceptible leaves had this tissue very loose in texture.—ERNST A. BESSEY.

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[17] GRUBER, EDUARD: Ueber das Verhalten der Zellkerne in den Zygosporen von *Sporodinia grandis* Link. Ber. d. deutsch. bot. Gesell. 19: 51–55. *pl.* 2. 1901.

[18] STURGIS, W. C.: Peach-foliage and fungicides. Report of the Connecticut Agricultural Experiment Station for the year ending October 31, 1900. Part III, pp. 219–254. *pls. 3–5.* 1901.

CLEISTOGAMOUS FLOWERS[19] are found in nearly all violets, but are especially typical in *Viola odorata*. The normal flower which appears early in the spring has a handsome corolla, but it seldom produces good seed. The inconspicuous cleistogamous flowers which come later, usually after the normal flowers have disappeared, produce an abundance of good seed. The stamens are larger in the normal flowers than in the cleistogamous, but the size of the pollen grains is about the same in both. The structure of the anther wall is quite different, the normal anther having the usual endothecium with lignified thickenings, while in the cleistogamous flower the endothecial layer retains its nucleus and cytoplasm.

After the pollen is mature there is a resting period of various duration. Pollen tubes are then put out which penetrate the wall of the anther at its upper part where there is a region of small cells rich in protoplasm, a tissue comparable to the conductive tissue of the style. *Oxalis acetosella*, *Linaria spuria*, and *Leersia oryzoides* were also studied.

In typical cleistogamous flowers the pollen germinates within the pollen sac, and the structure of the anther wall is modified to meet the new mode of pollination. In Linaria and Leersia, where the pollen was not observed to germinate within the pollen sac, the anther wall has the same structure as in the normal flower.—CHARLES J. CHAMBERLAIN.

BULLETINS from the experiment stations of interest to botanists, and not heretofore mentioned in these pages, are as follows: A. S. HITCHCOCK and G. L. CLOTHIER (Kans. no. 87, pp. 29) write upon the "Native agricultural grasses of Kansas," with many illustrations and charts of distribution. H. GARMAN writes on the agricultural grasses of Kentucky, with some fine reproductions from photographs, and A. M. PETER supplies some chemical analyses, the two articles forming one bulletin (Ky. no. 87, pp. 68, *pl. 14*).

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[19] DU SABLON, LECLERC: Recherches sur les fleurs cléistogames. Revue Générale de Botanique **12**: 305–318. *11 figs.* 1900.

F. A. WAUGH (Vt. no. 67, pp. 30) discusses hybridity among cultivated plums, and gives a systematic account of hybrid forms. Interesting trees of Vermont are described and figured by ANNA M. CLARK (Vt. no. 73, pp. 52), and those of Wyoming by AVEN NELSON (Wy. no. 40, pp. 52). W. W. ASHE (N. C. no. 175, pp. 8) gives technical diagnoses of 21 new species *Crataegus* and 8 new species of *Panicum*. E. E. BOGUE publishes "An annotated catalogue of the ferns and flowering plants of Oklahoma" (Okla. no. 45, pp. 48), D. A. SAUNDERS does the same for South Dakota (S. D. no. 64, pp. 127), and HENRY L. BOLLEY and L. R. WALDRON do the same for North Dakota (N. D. no. 46, pp. 91), all excellent beginnings toward complete floras of the respective states. C. F. WHEELER writes about the dwarf mistletoe in Michigan, with good reproductions from photographs, and on other topics (Mich. no. 186). L. H. PAMMEL describes the horse nettle (*Solanum Carolinense*), bind weed (*Convolvulus arvensis*), and ground burnut (*Tribulus terrestris*) as troublesome weeds in Iowa (Ia. no. 42.) D. A. BRODIE (Wash. no. 45, pp. 12) gives facts establishing the poisonous nature of the Oregon water-hemlock (*Cicuta vagans*).—J. C. ARTHUR.

FERTILIZATION IN *Ginkgo biloba* has recently been studied by Ikeno,[20] who gives a detailed account of phenomena from the cutting off of the ventral canal cell to the first division of the nucleus of the oospore. The nucleus of the ventral canal cell rapidly disorganizes, but in one instance it had enlarged *pari passu* with the nucleus of the oosphere. In preparations stained with methyl blue and acid fuchsin, the metaplasmic ground substance of the nucleus stains red, and the chromatin, which forms a small, irregular, granular mass, also takes the red, while the nucleoli stain blue. The nucleus then undergoes a great change in structure, so that the metaplasm and chromatin can no longer be distinguished from each other. The further development of the nucleus of the oosphere agrees with the description of the corresponding phenomena in *Pinus Laricio* as described by the reviewer in 1899. The tube nucleus and the nucleus of the stalk cell disorganize within the pollen tube and do not enter the oosphere, and it is very probable that only one of the male cells is discharged, the other disorganizing without being able to enter. The nucleus of the male cell slips out from the cytoplasm mantle before fusing with the nucleus of the oosphere. The mode of fusion is like that already described for *Cycas revoluta*, that is, the male nucleus gradually penetrates the egg nucleus before losing its own membrane. At the time of fusion the sex nuclei are very unequal in size, the female being about ten times as large as the male. The behavior of the chromatin during fusion is not described. The spindle in the first division of the fusion nucleus is very broad and multipolar, and is never parallel with the longitudinal axis of the oospore. In the case figured the spindle is transverse. Fertilization occurs while the ovules are still on the tree.—CHARLES J. CHAMBERLAIN.

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[20] Contribution à l'étude de la fécondation chez le *Ginkgo biloba*. Ann. Sci. Nat. Bot. VIII. **13**: 305–318. *pls. 2–3*. 1901.

DOUBLE FERTILIZATION in *Zea Mays*, which has been suspected for some time, and which is believed to be the cause of xenia, is described in a recent paper by Guignard.[21] The mature pollen grain contains, besides the vegetative nucleus, two very small elongated male cells, each in the form of a slender rod, curved or straight, and the ends often pointed. The cytoplasm of these cells is much reduced and difficult to distinguish, and their nuclei appear almost homogeneous. The synergids and oosphere are large, the former showing near the tip a conspicuous longitudinal striation, especially in material fixed in absolute alcohol. The nucleus of the oosphere is very large and contains much chromatin, and the cytoplasm is usually highly granular and much massed together at the time of fertilization. Near the oosphere, sometimes in the median plane, sometimes near the side of the embryo sac, are the two polar nuclei which do not fuse before fertilization, and have relatively large nuclei and a small amount of chromatin. As many as a dozen multinucleate cells may be found in the much narrowed antipodal end of the embryo sac. The pollen tube, after penetrating the embryo sac, usually seems to discharge its contents into one of the synergids. In one instance the two elongated male cells were observed resting against the base of a synergid; under high magnification their chromatin was distinct. One of the male cells unites with the oosphere, the other with the polar nuclei, which it binds together. Fertilization proceeds with such great rapidity that it could be observed in very few preparations. In general, the ovules at the base of the ear are first fertilized, and in hybrids many ovules are not fertilized. After fertilization one of the synergids usually persists for a time, with the contents finely granular and refractive. Division of the definitive nucleus proceeds so rapidly that the author was not able to follow the course of cell division. The first two nuclei of the endosperm are large, each one having an enormous nucleolus and many smaller nucleoli. It is to be regretted that no figures are given.—W. J. G. LAND.

THE EMBRYOLOGY of the Balanophoraceae presents many puzzling peculiarities. Accounts are somewhat divergent, but whether the divergence is due entirely to variation in the processes still remains to be seen. Writers agree that there is no ovule or placenta in Balanophora but that the megaspore is situated in a tissue at the base of a prolongation incorrectly termed a "style." Van Tieghem (1896) found that in *B. indica* the polar nuclei do not fuse and that fertilization occurs at the antipodal end of the sac as often as at the upper end.

According to Treub (1898) in *B. elongata* the megaspore germinates in the usual manner. The polar nuclei, however, do not fuse but each divides independently. The egg apparatus breaks down and there is no fertilization, but an embryo develops from one of the cells of the endosperm. Lotsy (1899) investigated *B. globosa* and supported Treub in every particular, including the peculiar origin of the embryo.

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[21] La double fécondation dans le mais. Jour. Bot. 15:1–14. 1901.

Chodat and Bernard have recently investigated *Helosis guayanensis.*[22] The archesporial cell becomes the megaspore directly without cutting off a tapetal cell or giving rise to a row of potential megaspores.

The jacket or "tapetum" surrounding the embryo sac is sporogenous tissue. The two daughter nuclei resulting from the first division of the nucleus of the megaspore are quite different in appearance, the one at the upper end of the sac staining much more deeply. This nucleus gives rise to the egg, two synergids, and a polar nucleus in the usual manner. The other nucleus stains faintly and rarely divides at all, but soon degenerates so that no antipodals or polar nucleus are formed. According to Van Tieghem, the egg is fertilized in Helosis and Balanophora.

The present writers find that in Helosis the egg becomes large, but also becomes very weak and feeble in appearance, so that while they were not able to prove or disprove the occurrence of fertilization, they believe that the feeble condition of the egg together with the position of the embryo in the endosperm favor Treub's view that the embryo arises apogamously from the endosperm.—CHARLES J. CHAMBERLAIN.

ITEMS OF TAXONOMIC interest are as follows: E. P. BICKNELL (Torreya **1**: 25-28. 1901) has described a new Triosteum (*T. aurantiacum*) from the northeastern United States.—*Pl. Bakerianae* **2**: 1-42. 1901 contains Baker's collection of 1899, from fungi to grasses. Numerous new fungi are described by F. S. EARLE.—ALICE EASTWOOD (Bull. Torr. Bot. Club **28**: 137-160. *pls. 15-20.* 1901) has published upon some small-flowered species of Nemophila from the Pacific coast, describing twenty-six new species.—M. A. HOWE (*idem* 161-165) has described a new Riccia from Georgia.—E. P. BICKNELL (*idem* 166-172) has revised the eastern species of Teucrium, recognizing six species and describing four as new.—P. A. RYDBERG (*idem* 173-183), in further studies of the Potentilleae, describes new species of Potentilla (8), Horkelia, and Drymocallis.—W. A. SETCHELL (Zoe **5**: 121-129. 1901), in his "Notes on Algae," has described two new genera of Laminaceae (*Hedophyllum* and *Pleurophycus*) and a new genus of Dumontiaceae (*Weeksia*), besides several new species in other genera.—A. ENGLER (Bot. Jahrb. **36**: 29-126. 1901), in his 21st contribution to the African flora, presents the following papers: Fungi by P. HENNINGS, who describes numerous new species and two new genera, *Fistulinella* (Polyporaceae) and *Lactariopsis* (Agaricaceae); Algae by W. SCHMIDLE; a revision of Schrebera (Oleaceae) by E. GILG;

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[22] CHODAT, R., and BERNARD, C.: Sur le sac embryonnaire de l'Helosis guayanensis. Jour. de Botanique **14**: 72-79. *pls. 1-2.* 1900.

Leguminosae by H. HARMS, *Scorodophloeus*, *Rhynchotropis*, and *Schefflerodendron* being new genera; Myrsinaceae by E. GILG; Amarantaceae by G. LOPRIORE, *Argyrostachys* being a new genus; Acanthaceae by G. LINDAU; Caricaceae by I. URBAN, *Cylicomorpha* being a new genus; and Gramineae by R. PILGER.—CARL MEZ (*idem* Beibl. **30**: 1–20. 1901) has described numerous new species of Bromeliaceae and Lauraceae.—I. URBAN (*idem* 27–38) continues his papers on new American plants.—A. ENGLER (*idem* 42) has described a new genus of Araceae (*Protarum*) from the Seychelles.—B. D. GILBERT (Fern Bulletin **9**: 27. 1901) has described a new variety of *Botrychium ternatum* (*Oneidense*) from central New York.—ACHILLE FORTI (Ber. deut. bot. Gesell. **19**: 6–7. 1901) has published a new genus (*Heteroceras*) of marine Peridineae.—W. SCHMIDLE (*idem* 20–24) has described a new genus (*Coccomyxa*) of the Protococcoideae.—C. S. SARGENT (Rhodora **3**: 71–79. 1901) has described six new species of Crataegus from the Province of Quebec near Montreal.—G. P. CLINTON (*idem* 79–82) has described two new smuts on *Eriocaulon septangulare*.—E. L. GREENE (*idem* 83–84) has segregated from *Eupatorium ageratoides* the bulk of the New England and northern forms that pass under that name, and called the species *E. boreale*.—C. DE CANDOLLE (Bull. Herb. Boiss. II. **1**: 353–366. 1901) has published an account of the Brazilian Piperaceae and Meliaceae collected by W. Schwacke, including descriptions of numerous new species.—R. CHODAT (*idem* 395–442), in continuing his account of the Hassler collection from Paraguay, has described numerous new species in various families.—W. TRELEASE (Rep. Mo. Bot. Gard. **12**: 77. *pl. 34*. 1901) has described a new cristate variety of *Pellaea atropurpurea* from Missouri.—J. W. TOUMEY (*idem* 75–76. *pls. 32–33*) has described a new Agave from Arizona. H. M. RICHARDS (Bull. Torr. Bot. Club **28**: 257–265. *pls. 21–22*. 1901) has described a new genus *Ceramothamnion*) of red algae from Bermuda.—P. A. RYDBERG (*idem* 266–284) has published a fifth fascicle of new species from the Rocky mountain region, among them being *Piperia*, a new genus of orchids.—J. K. SMALL (*idem* 290–294) has published a third paper on the shrubs and trees of the southern states, including a revision of the southeastern species of *Ptelea*.—In Torreya (**1**: 54–55. 1901) J. K. SMALL has published a new *Cornus* from Kentucky, and N. L. BRITTON a new *Crataegus* from Washington.—F. LAMSON-SCRIBNER and E. D. MERRILL (Rhodora **3**: 93–128. 1901) have published a revision of the New England species of *Panicum*, recognizing thirty-five species.—J. K. SMALL (Bull. N. Y. Bot. Garden **2**: 89–101. 1901) has published a synopsis of the Mimosaceae of the southeastern United States. He recognizes fourteen genera, and among them *Siderocarpos* and *Havardia* have been separated from Pithecolobium as new.—M. A. HOWE (*idem* 101–105. *pl. 14*) has published an enumeration of the liverworts collected in the Yukon Territory by R. S. Williams in 1898–9, including a new species of

Scapania. MR. WILLIAMS himself (*idem* 105–148. *pls. 15–24*) has enumerated the mosses, including a new genus (*Bryobrittonia*) closely related to Tortula and Desmatodon, and a number of new species. L. M. UNDERWOOD (*idem* 148–149). enumerates the pteridophytes; while the seed plants are presented by N. L. BRITTON and P. A. RYDBERG (*idem* 149–187), numerous new species being described.—P. A. RYDBERG (*idem* 187–233 *pls. 25–33*) has given an account of the oaks of the continental divide north of Mexico, recognizing twenty-nine species, nine of which are new.—J. M. C.

PROFESSOR A. B. MACALLUM[23] has recently added an interesting contribution to the cytology of certain so-called non-nucleated organisms. His work is divided into three parts, each dealing with a separate group of low organisms—the Cyanophyceae, Beggiatoa, and the yeast cell—and was undertaken with the hope of throwing some light on the origin of the cell nucleus, and to obtain data to determine the morphological character of the primal life organism. In his investigations Macallum not only used the ordinary cytological methods, but microchemical tests were also employed to advantage. Picric acid and corrosive sublimate afforded the best results as fixing fluids. The stains that gave the best differentiation were Ehrlich's and Delafield's haematoxylin, Czokor's alum cochineal, saffranin, eosin, picro-carmin, and methylen-blue. The microchemical methods employed for obtaining the reactions for "masked iron" were practically the same as those used in his earlier work published in 1896. The iron liberated by sulfuric acid alcohol was converted into Prussian blue, the trichomes were then stained with a picro-carmin solution for twenty-four hours, when the cyanophycin granules acquired a deep red color which contrasts markedly with the Prussian blue tint of the iron-holding granules. The results obtained on the Cyanophyceae are briefly as follows. The cell consists of two portions, the central body and the peripheral zone holding the pigment. There is no evidence of the presence of a special chromatophore. There are two types of granules present in the cell. The one stains with haematoxylin, contains "masked iron" and organic phosphorus, and therefore resembles chromatin. The other type is found in the peripheral layer, and chiefly adjacent to the cell membrane. It stains with picro-carmin, and is free from organic phosphorus and "masked iron." It is probably a proteid. There is no nucleus or any structure which resembles a nucleus in the Cyanophyceae. In Beggiatoa there is no differentiation of the cytoplasm into a central body and a peripheral layer, such as Bütschli describes. The compounds of "masked iron" and organic phosphorus are uniformly diffused throughout the cytoplasm in the threads. In the "spirilla," "comma," and "coccus" forms the cytoplasm shows characters like those of the threads, but there are also granules present which give a slight reaction for "masked iron" and organic phosphorus, and therefore are considered analogous to chromatin. No specialized chromatin-holding structure in the shape of a nucleus was found in any of the forms of Beggiatoa studied. In his studies on the yeast cell, Macallum finds that the cytoplasm takes a stain with haematoxylin and gives a diffuse reaction for "masked iron" and organic phosphorus. In addition to the chromatin-like substance diffused throughout the cell, there is usually present a homogeneous corpuscle. This is not considered to be a nucleus, although held to be such by other investigators. The chromatin-like substance in Saccharomyces is soluble in artificial gastric juices, thus differing from the chromatin of the higher plant and animal cells. The paper is illustrated by a colored lithographic plate. It is a valuable and highly interesting addition to the literature of this important problem.—A. A. LAWSON.

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[23] On the cytology of non-nucleated organisms. University of Toronto studies. Physiological series 2. 1900.

NEWS.

Dr. G. T. Moore, of Dartmouth College, has been appointed phycologist in the Department of Agriculture.

Dr. J. C. Arthur sailed July 6 and will spend July and August in Europe with his bride. He will attend the botanical conference at Geneva in August.

Dr. J. B. Overton, who received his doctorate in June from the University of Chicago, has been appointed professor of botany in Illinois College, at Jacksonville.

Mr. A. A. Lawson, fellow in botany at the University of Chicago during the past year, has been appointed assistant in botany in Leland Stanford Junior University.

M. Henri Philibert, honorary professor in the Faculty of Letters, distinguished for his bryological studies, died at Aix on the fourteenth of May, in his seventy-ninth year.

Professor G. J. Peirce, of Leland Stanford Junior University, takes charge of the botanical work during the summer at the Hopkins Seaside Laboratory near Pacific Grove, California.

We learn from *Science* that a memorial tablet of the late Thomas Conrad Porter, long professor of botany in Lafayette College, was unveiled in connection with the recent commencement exercises.

Professor C. E. Bessey, after attending the meeting of the American Association for the Advancement of Science in Denver, will go to the Pike's peak region to join the University of Nebraska camp for a month, to study the mountain flora.

The regents of West Virginia University have abolished the professorship of botany in that institution without notice to the present incumbent, Dr. E. B. Copeland. Dr. Copeland will spend the summer at the Cold Spring Biological Laboratory.

Mr. H. N. Whitford, assistant in botany in the University of Chicago, has been appointed a collaborator of the Bureau of Forestry for the study of the ecology of the forest. He is to carry on work this summer in the neighborhood of Flat Head lake, Montana.

Dr. H. C. Cowles, of the University of Chicago, will conduct a field party during August in northwestern Montana. The party will number about twenty, and the work will be along ecological lines. Most of the work will be in the neighborhood of Flathead lake, where the state biological station is located.

THE AMERICAN ASSOCIATION for the Advancement of Science will meet at Denver, Colorado, August 23-28, 1901. A preliminary program of the meetings of section G (Botany) will be issued about July 15. One day will be given up to a joint session with the Botanical Society of America. It is also planned to devote one day's program to the subject "Adaptations of desert plants."

DR. F. E. CLEMENTS is to spend the summer in the Pike's peak region in Colorado, engaged in ecological studies of the flora. He will be accompanied by a party of botanists from the University of Nebraska, numbering a dozen or more. Instruments for accurate observation of ecological factors have been provided for the party.

THE LATEST *Bulletin* of the New York Botanical Garden, issued May 27 last, contains much information of interest to botanists. The planting of the grounds is proceeding rapidly, and the present showing of species grown during the year is as follows: herbaceous grounds 2300, fruticetum 450, salicetum 40, arboretum 220, and viticetum 60. During the year 48,895 specimens have been added to the herbaria.

JOHN J. THORNBER has been appointed special botanical collector for the University of Nebraska for the summer of 1901. He is to accompany the field party of the United States Forestry Division now at work in Nebraska, and is to act as its botanist, at the same time being the botanical representative of the university. In addition to the collection of specimens, he is to make careful ecological studies throughout the territory traversed.

UNDER A commission from the United States government, Dr. H. von Schrenk, of the Shaw School of Botany, is to spend the summer in Europe, in an investigation of the problems connected with the decay of railroad ties on the principal roads, this work being done in connection with an extensive series of investigations into the same subject which he is undertaking for the Department of Agriculture and in which the principal American railroads are cooperating.

ON MAY THIRTIETH there occurred the unveiling of a memorial tablet to Asa Gray in the Hall of Fame of the University of New York. The ceremony was committed to the Botanical Society of America. Most appropriately Dr. B. L. Robinson, professor of systematic botany in Harvard University and curator of the Gray herbarium, and Dr. N. L. Britton, director of the New York Botanical Garden, were appointed to act as representatives of the society, Dr. Robinson unveiling the tablet.

SUMMER FIELD WORK will be undertaken by the staff of the School of Botany of the University of Texas as follows: One party will make an exploration of Padre island between Corpus Christi and Brownsville. A member of the staff will accompany a party conducting the mineralogical survey, which will make an expedition into the trans-Pecos region of the state. A party of students will collect plants and study ecological questions from Cuero westward toward the Pecos river. These various expeditions should do much in making known the state botanically.

THE BOTANICAL staff in the State University of Iowa has organized a summer school of botany to be conducted along the shores of Lake Okoboji in northern Iowa. The region is not only one of the most delightful of western summer resorts, but has unusual attractiveness for the naturalist. The university offers this year to students of botany a laboratory with all essential apparatus and libraries. Abundant boats put all the lakes into easy communication with one aaother, and in addition the laboratory will have its own equipment for the use of students. Professor Shimek will act as director and will be aided by special assistants. It is expected that hereafter the work in botany for the summer session of the State University of Iowa will all be conducted at Okoboji.

DR. J. N. ROSE left about the 20th of June for his third botanical trip to Mexico. He expects to go first to the City of Mexico, working out from this point as a base southward towards Acapulco and eastward toward Vera Cruz, probably ascending Mount Orizaba and Popocatepetl. The objects of his trips are to make a general botanical collection; to collect at type localities certain species of Humboldt, Galeotti, Schiede, and other early collectors; and to acquire information regarding the economic uses of Mexican plants, especially such as will supplement a second paper on the useful plants of Mexico, which is now nearly completed.

ERRATA in the last volume reported too late for inclusion in the usual list are as follows:

P. 109, line 4, after pellucido-punctata insert comma.
P. 121, line 8 from below, after corticata insert comma.
P. 392, line 14, for ERIGERON read ERIOGONUM.
P. 393, line 6, for TROGANUS read TIOGANUS.
P. 439, line 24, for position and negation read positive and negative.

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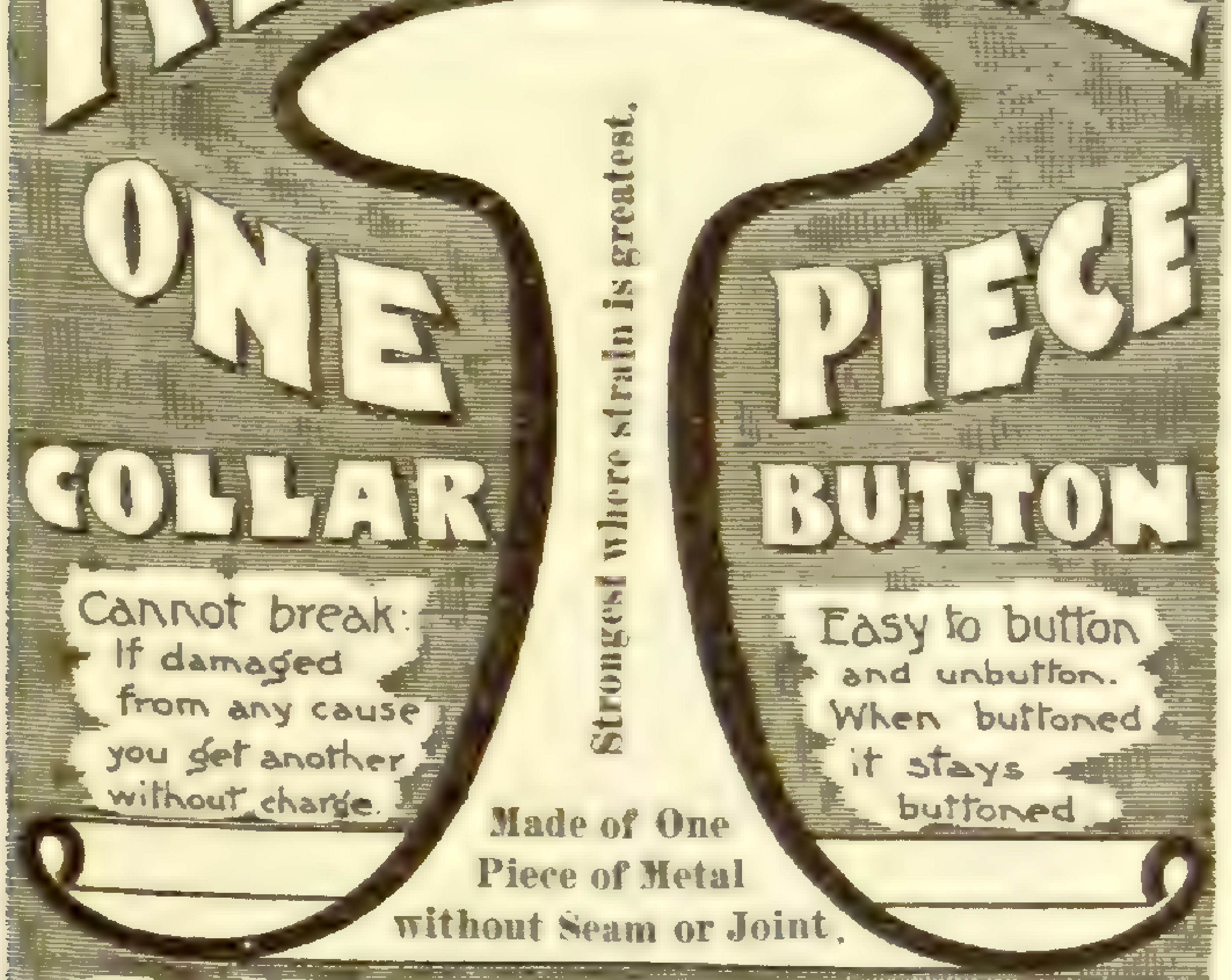
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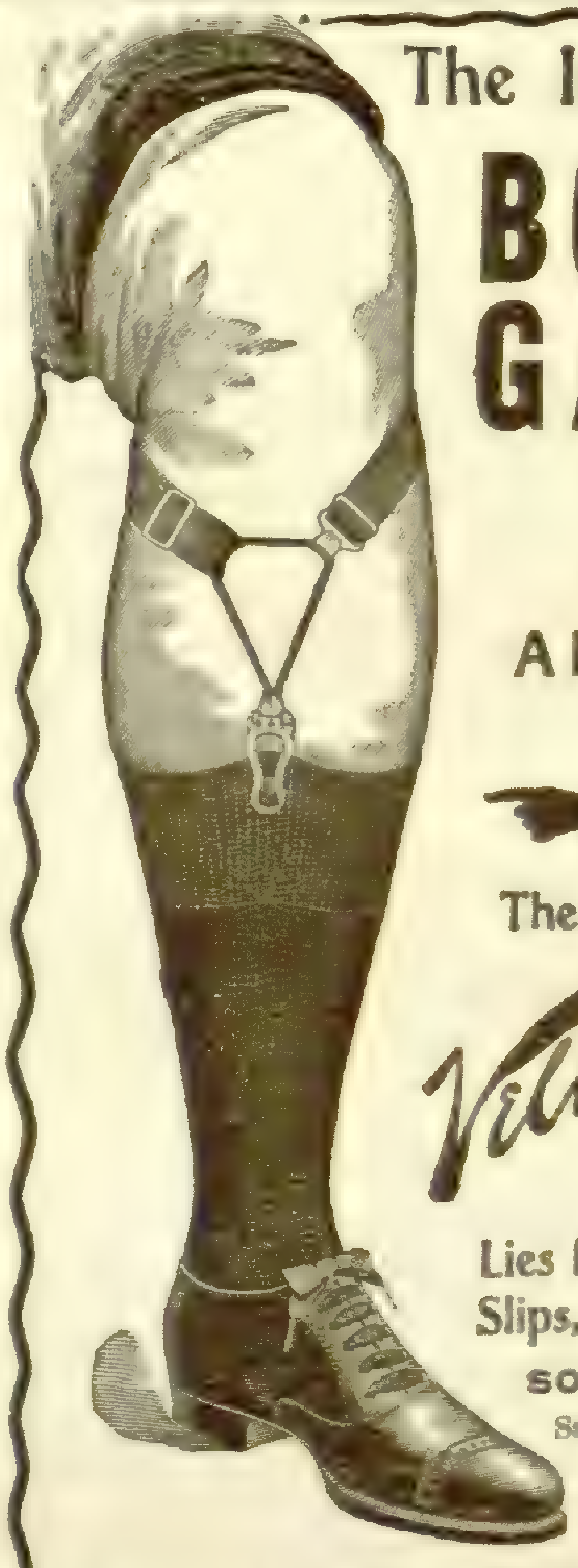

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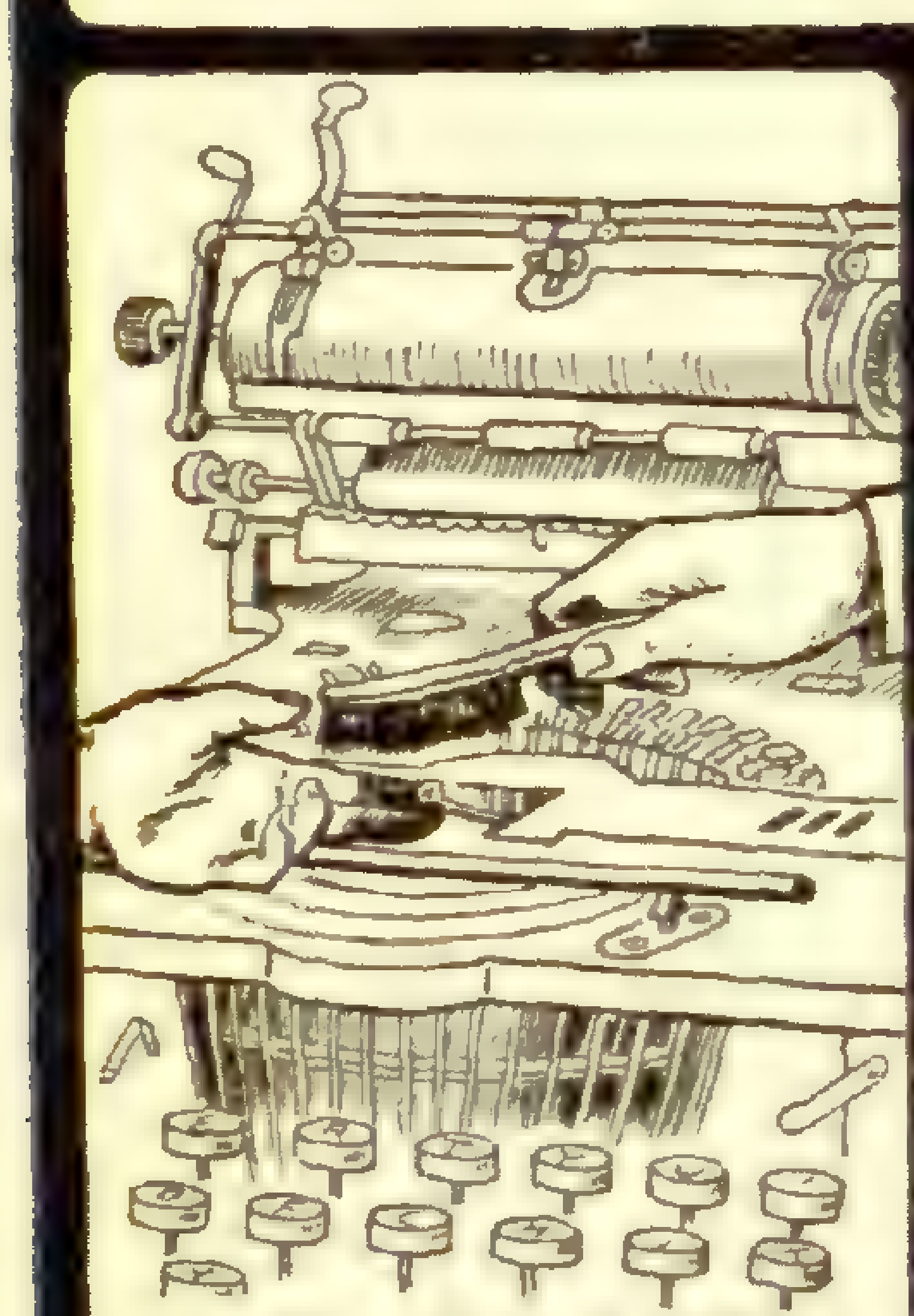

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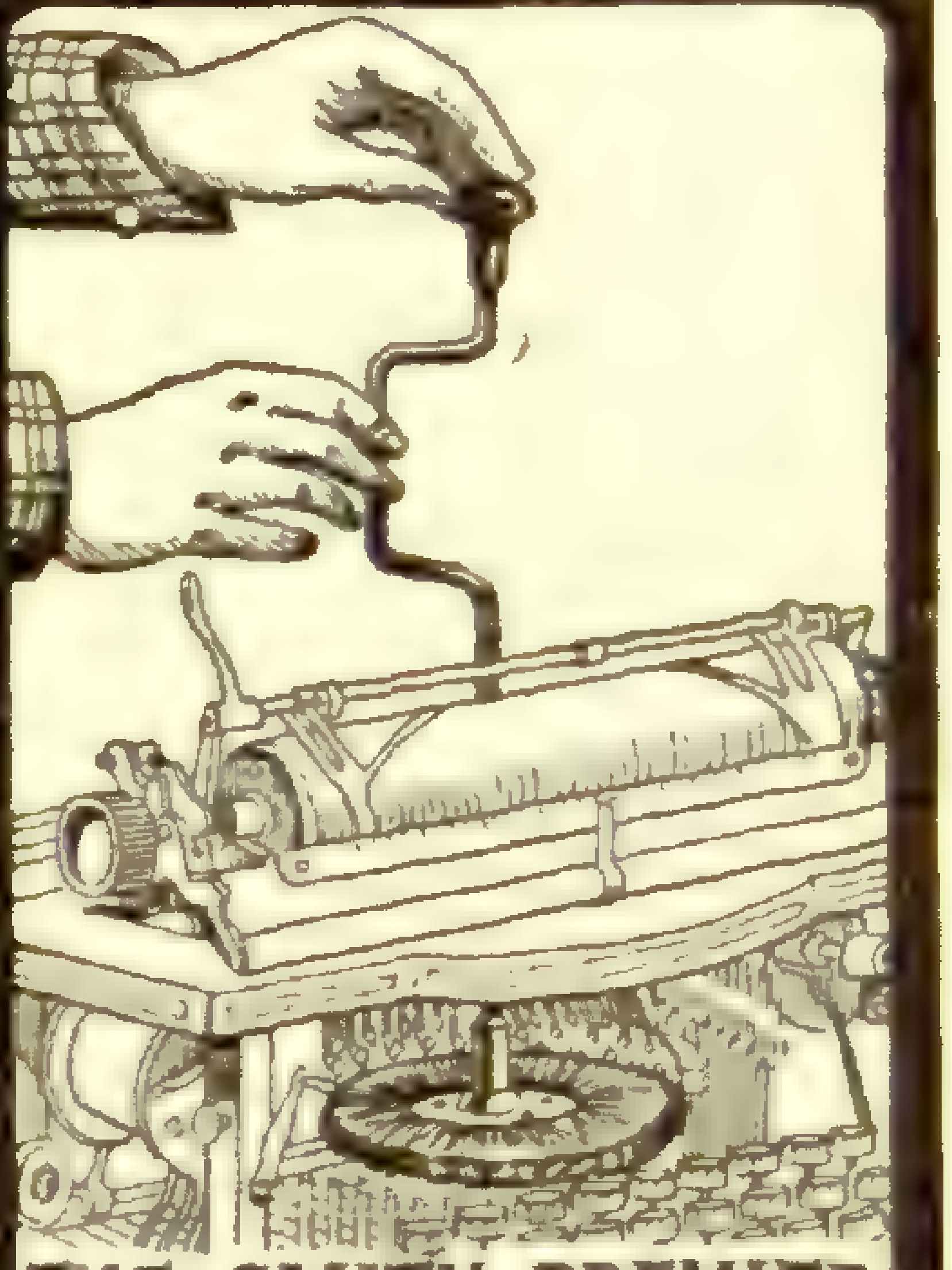

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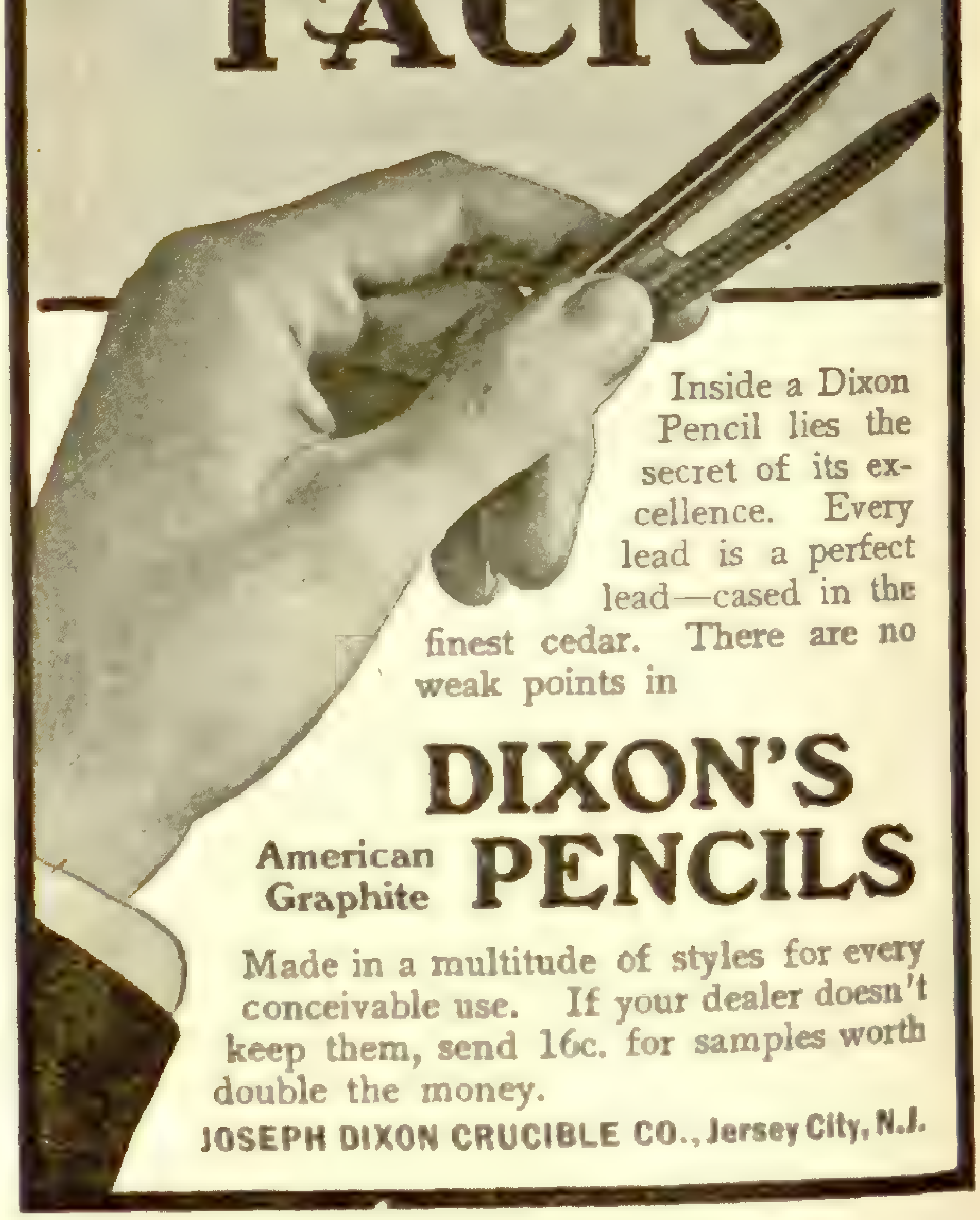

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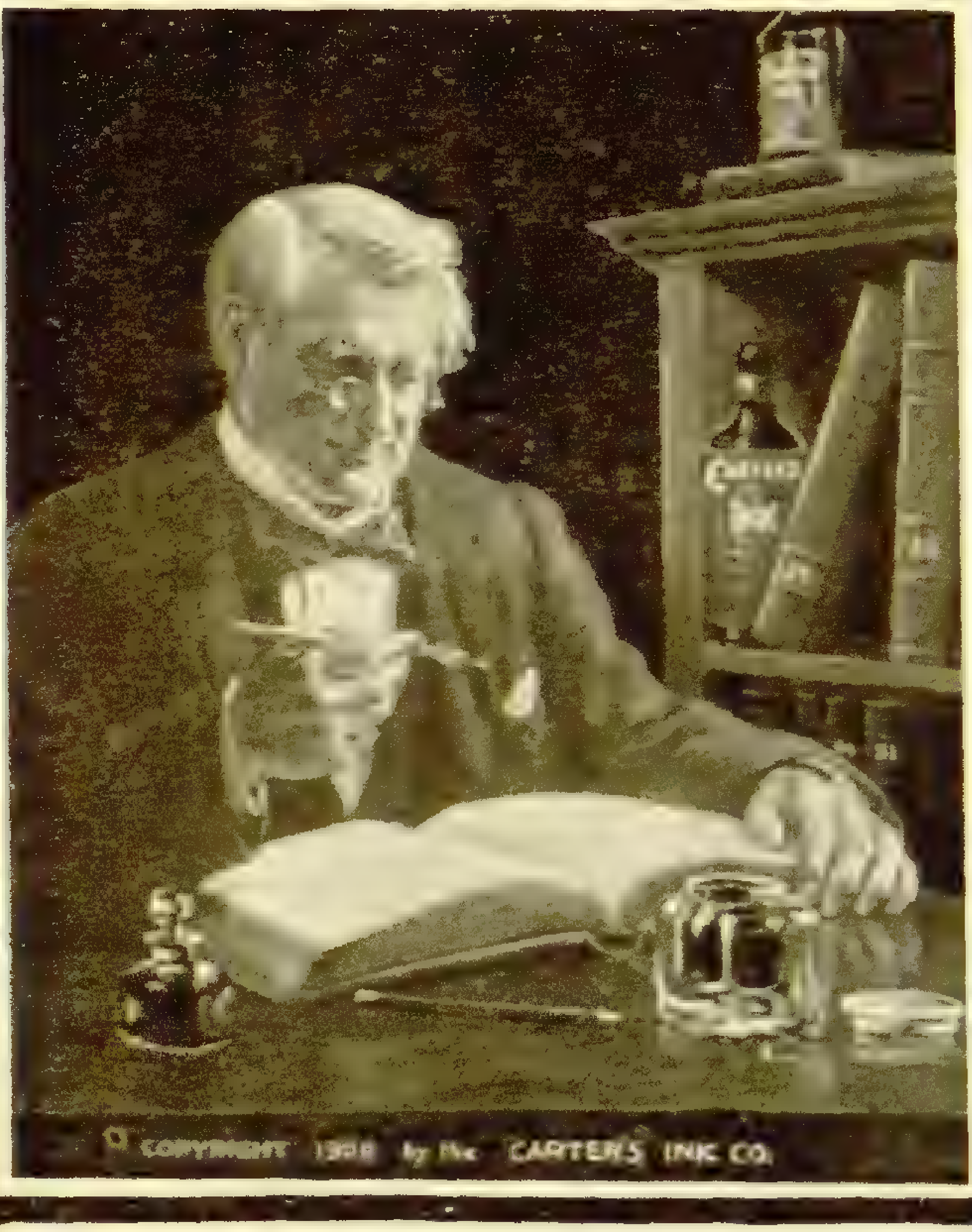

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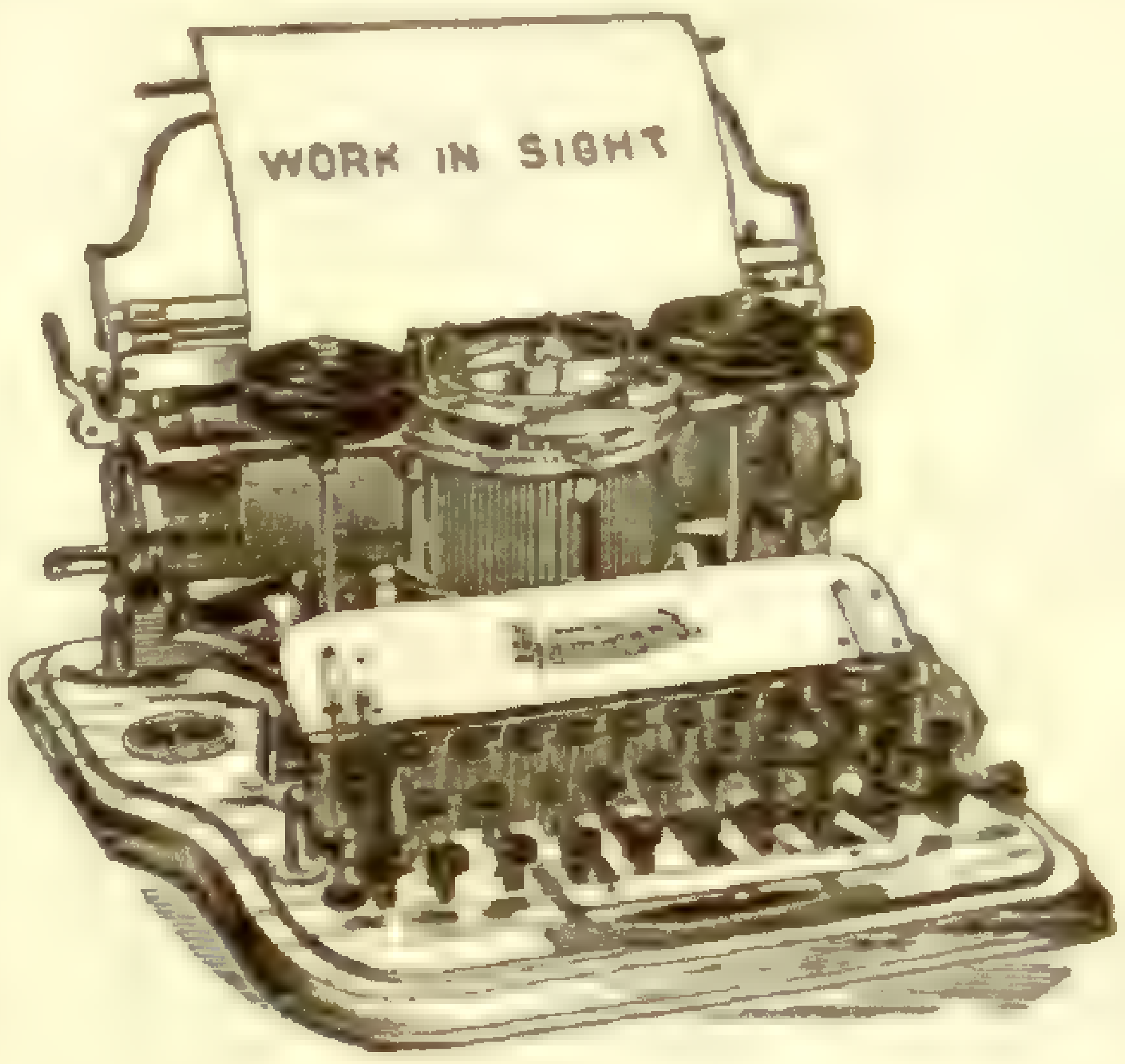

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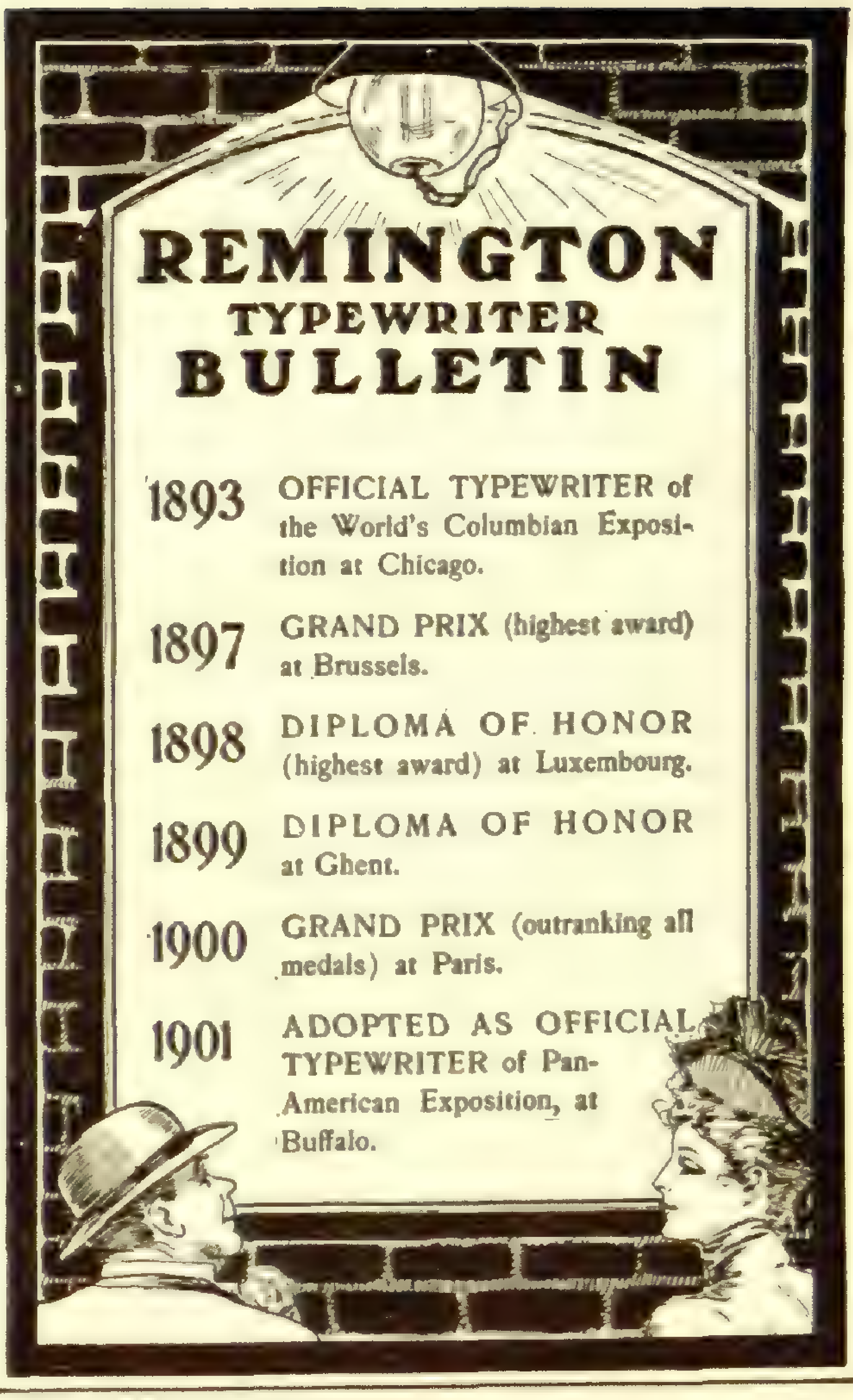

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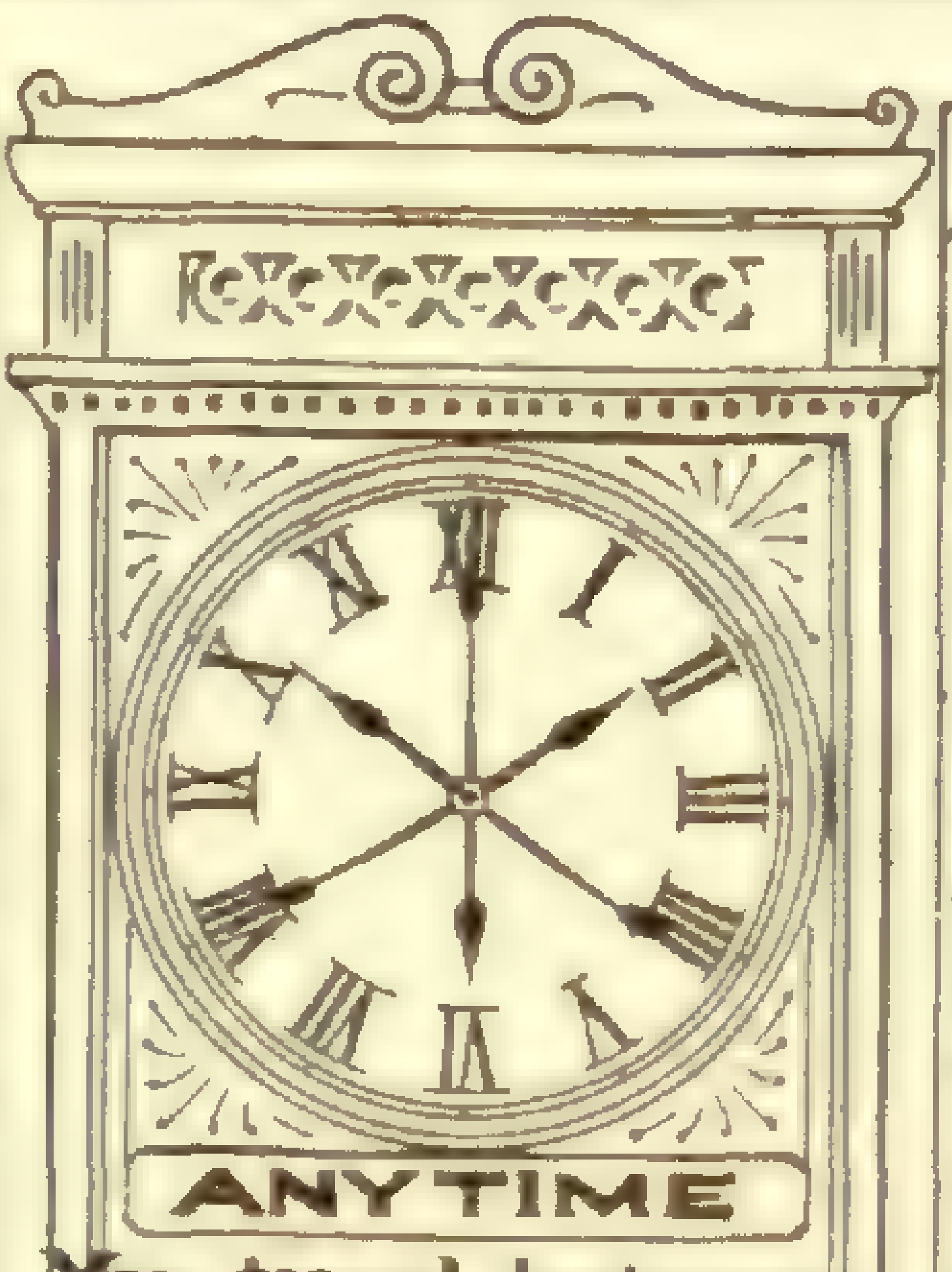

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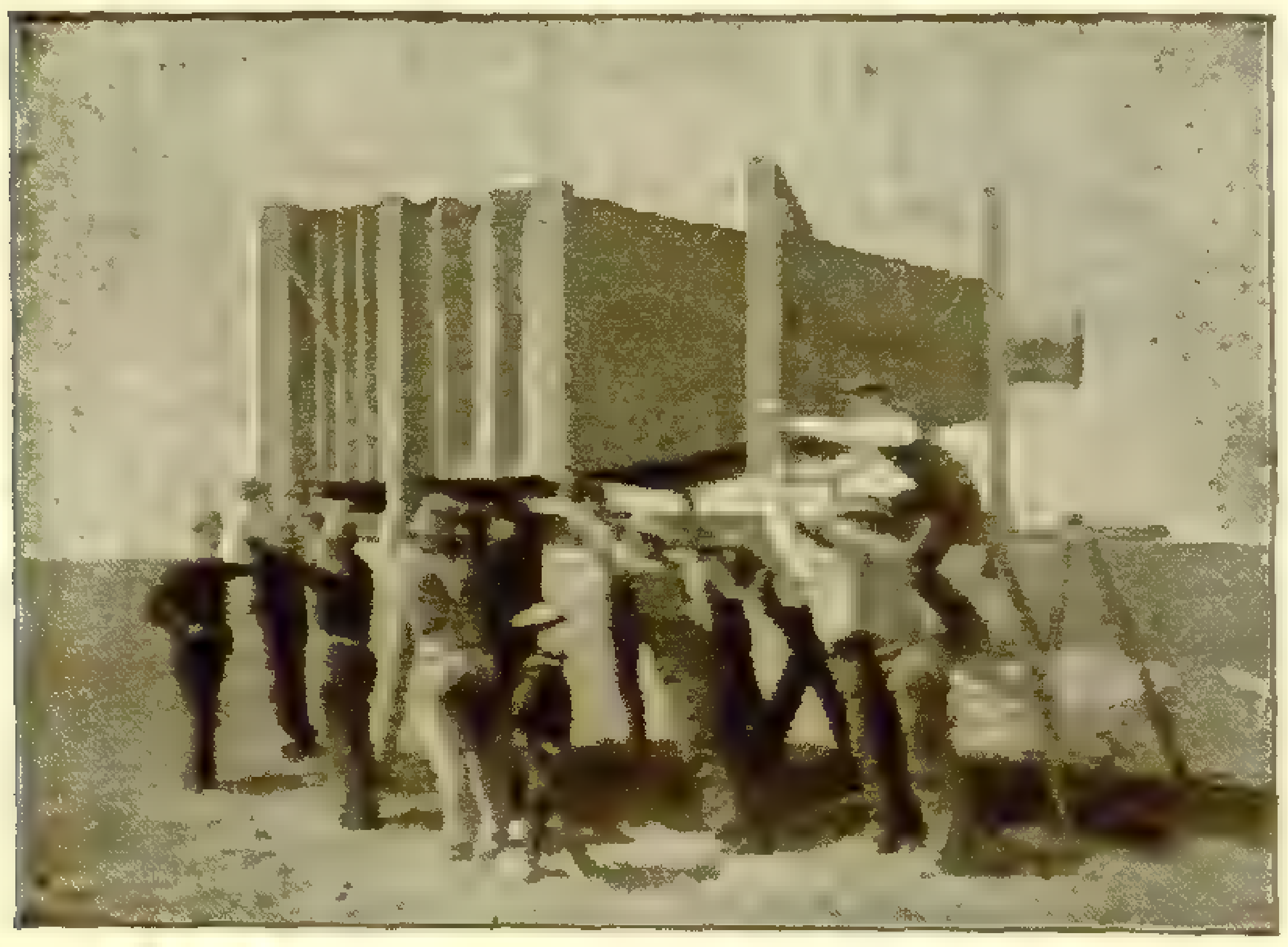

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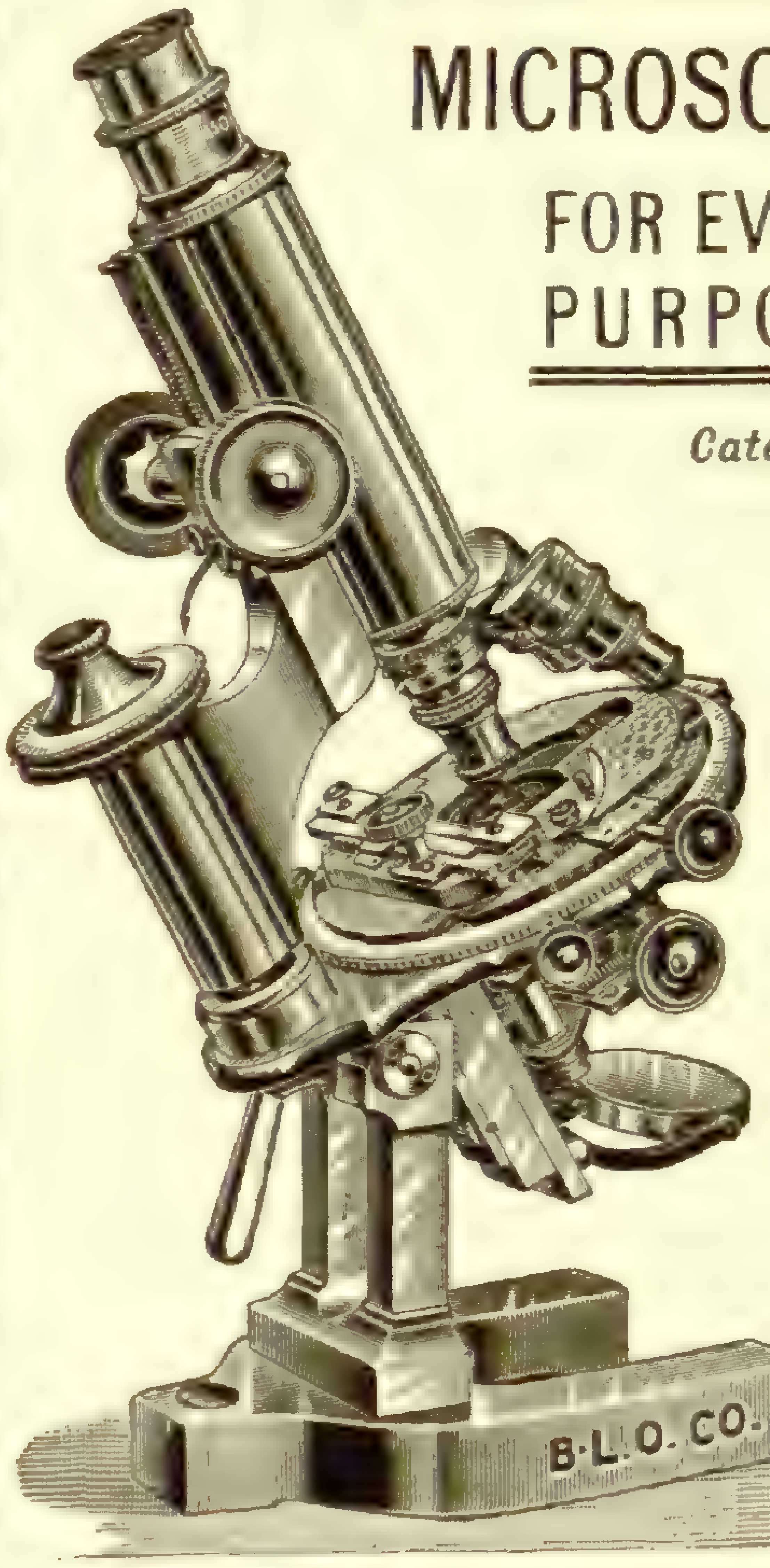

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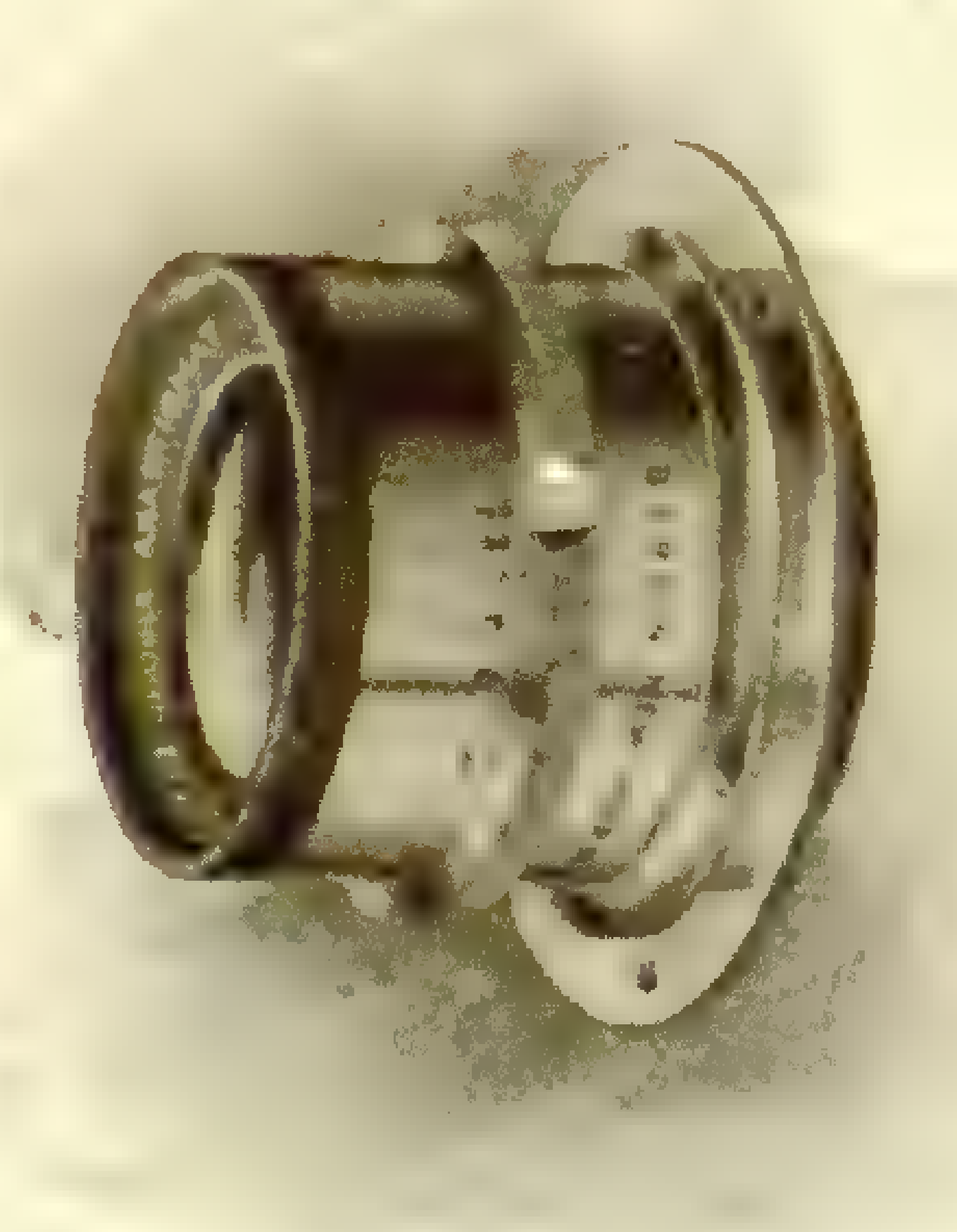

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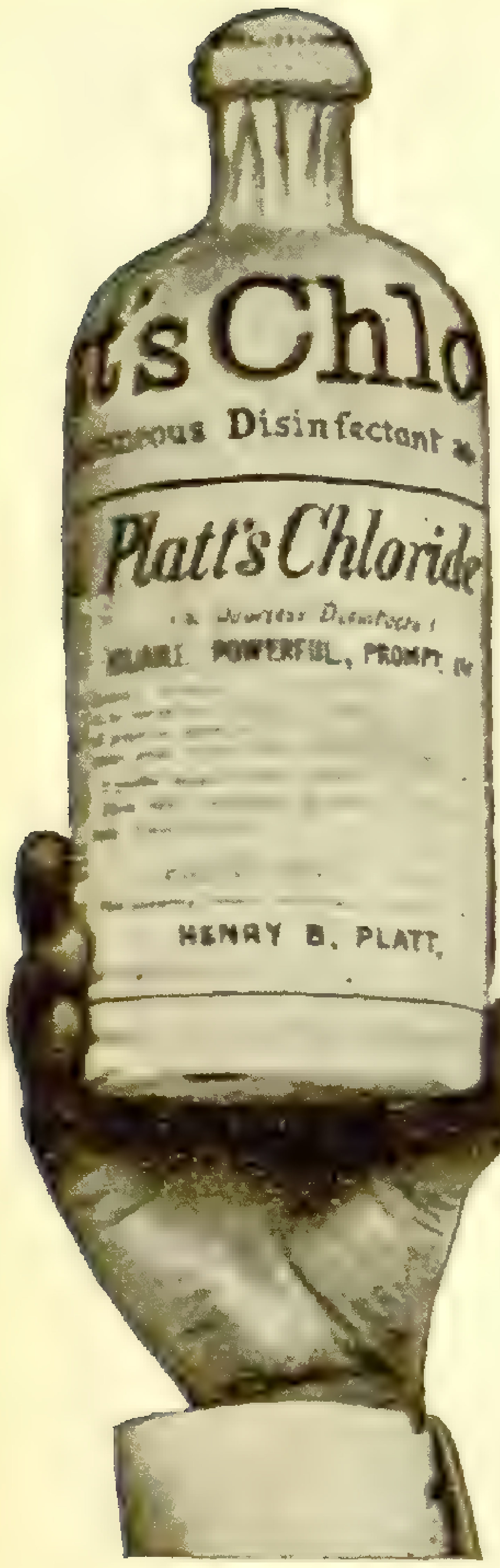

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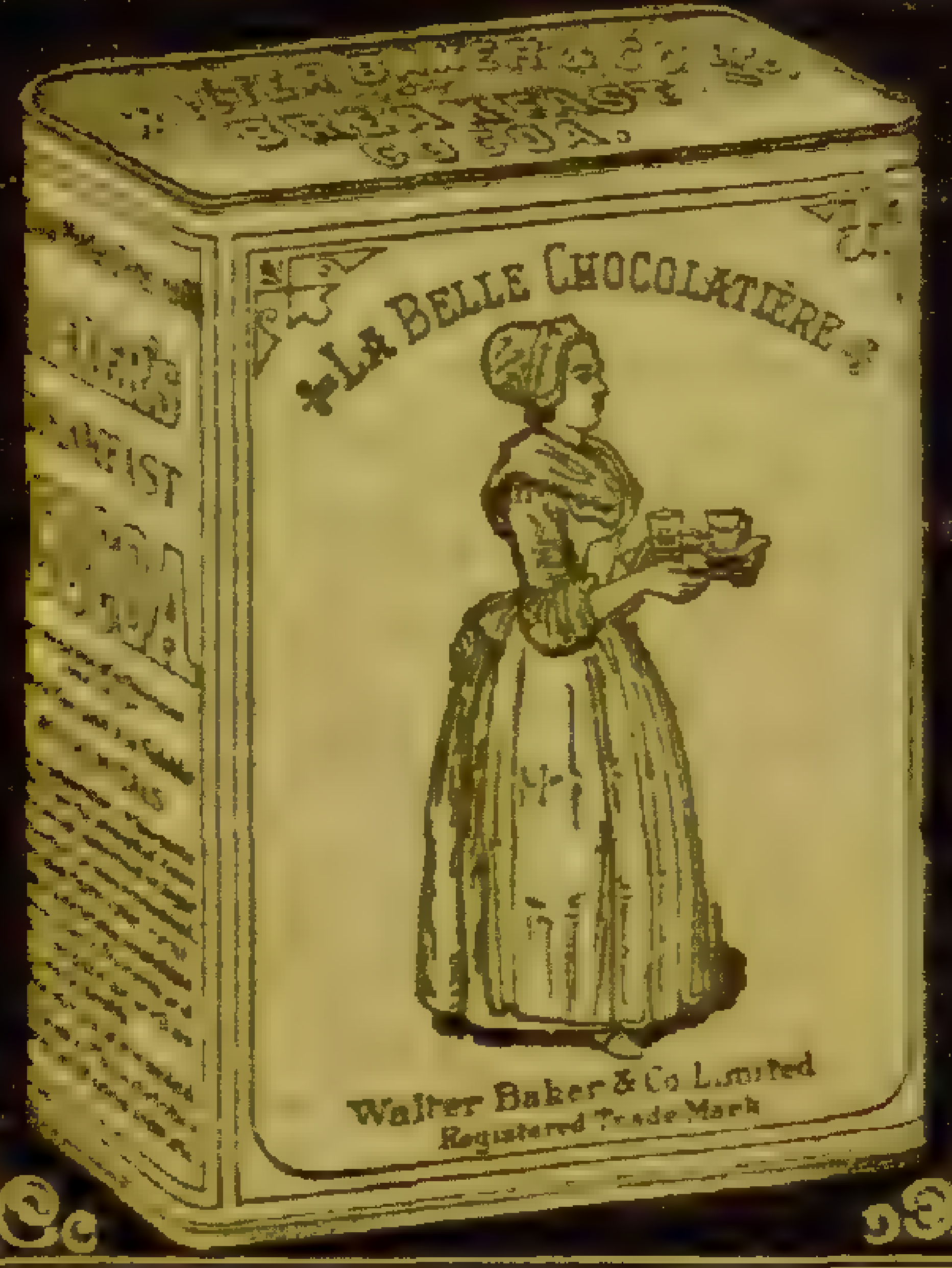
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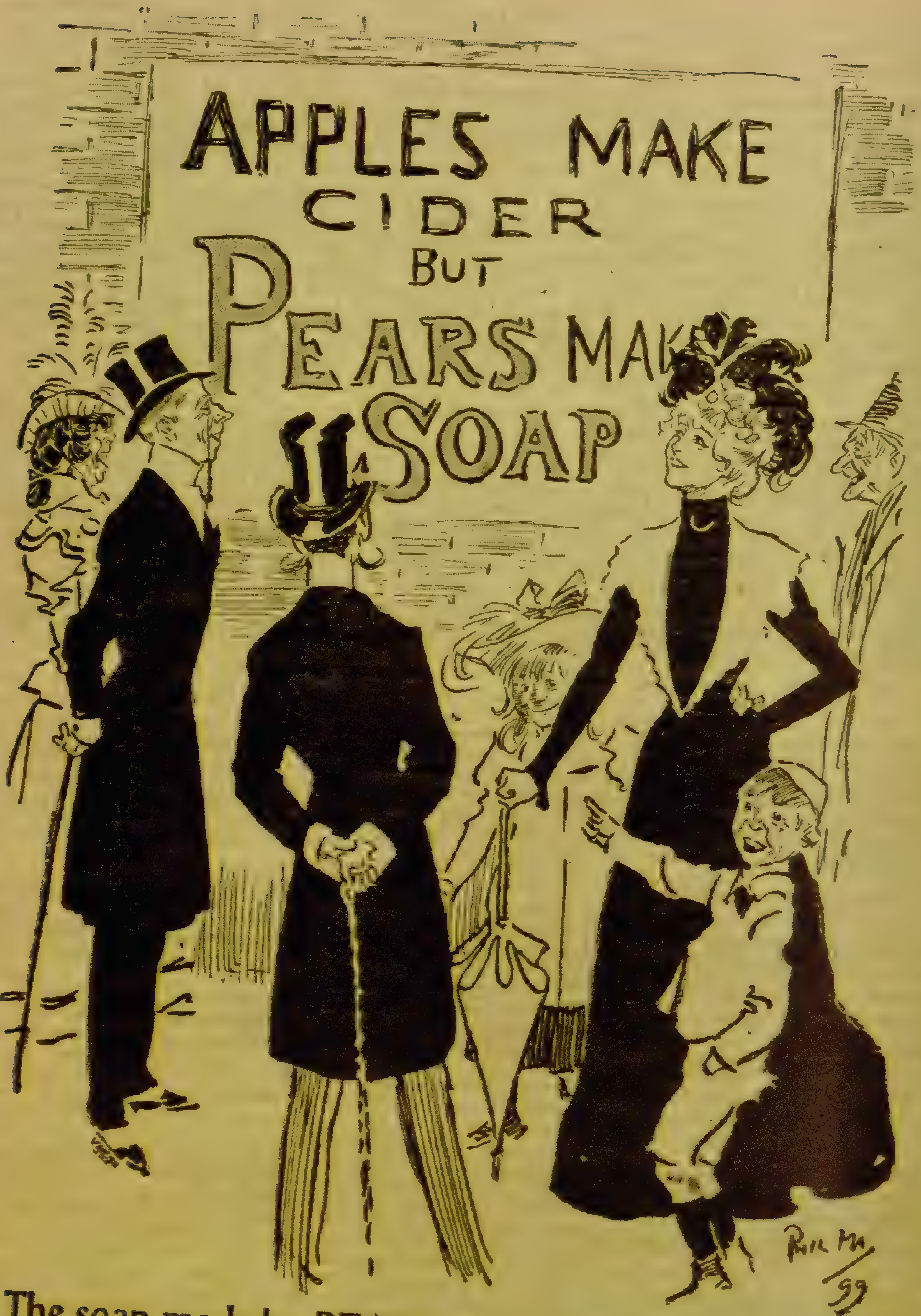

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CONTENTS

GAMETOGENESIS AND FERTILIZATION IN ALBUGO. Contributions from the Hull Botanical Laboratory. XXIX. (with plates I–IV.) *Frank Lincoln Stevens* 77

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS. Contributions from the Hull Botanical Laboratory. XXX. (with twenty-four text figures.) *William L. Bray* - - - - - - - - 99

A STUDY OF THE SPORANGIA AND GAMETOPHYTES OF SELAGINELLA APUS AND SELAGINELLA RUPESTRIS. Contributions from the Hull Botanical Laboratory. XXXI. (with plates V–IX.) *Florence May Lyon* - - - 124

BRIEFER ARTICLES.

The Probable Function of Calcium Oxalate Crystals in Plants. *Albert Schneider* 142

CURRENT LITERATURE.

BOOK REVIEWS - - - - - - - - - - - - 145

Perception and Propagation of Stimuli in Roots

Two New Books on Plant Physiology

MINOR NOTICES - - - - - - - - - - - - 150

NOTES FOR STUDENTS - - - - - - - - - - 151

NEWS - - - - - - - - - - - - - 154

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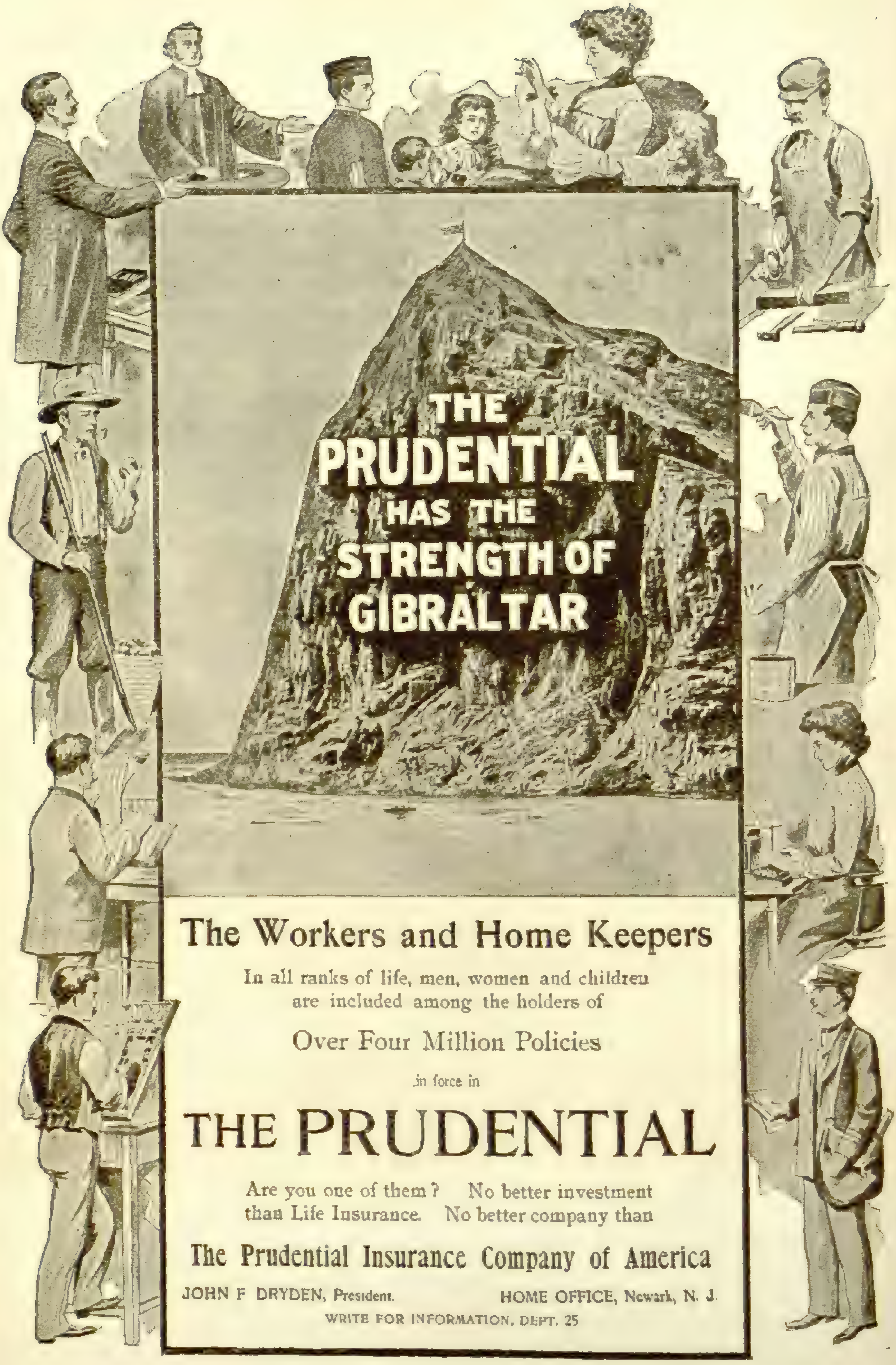
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VOLUME XXXII NUMBER 2

BOTANICAL GAZETTE

AUGUST, 1901

GAMETOGENESIS AND FERTILIZATION IN ALBUGO.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX.

FRANK LINCOLN STEVENS.

(WITH PLATES I-IV)

BEFORE the publication of my paper (1899) describing the fertilization of *Albugo Bliti*, the mature oosphere in the Phycomycetes was generally conceded to be a uninucleate structure. The question of homologies in the group did not then seem difficult. *A. Bliti*, however, presented a unique condition, in that about one hundred antheridial nuclei fuse in pairs with an equal number of egg nuclei. This condition seemed remarkable and inexplicable, inasmuch as Wager (1896) had studied the fertilization in *A. candida*, and had described a fusion of single male and female nuclei in a uninucleate oosphere. Such divergence in the same genus led to some speculation. Davis (1900) reexamined *A. candida* and fully confirmed Wager's account, as indeed Berlese (1898) had already done. It is well established, therefore, that there is a simple fusion in *A. candida*, and my own account (1899) stands for a multiple fusion in *A. Bliti*. Interest also attaches to this genus on account of the presence of a coenocentrum, a structure of prominence, but of hitherto unknown function.

The study of *A. Portulacae* and *A. Tragopogonis* was undertaken in the hope that these species might help to explain the apparent discrepancy between the two species previously studied. The selection of *A. Tragopogonis* has proved particularly fortunate, for it has led directly to a solution of the problem. The conditions in this species, while to a certain extent similar to those described for *A. candida*, made evident the necessity of a critical reexamination of the latter. I have included *A. candida*, therefore, in this investigation.

The material of *A. Portulacae* on *Portulaca oleracea*, and *A. Tragopogonis* on cultivated *Tragopogon* and *Ambrosia artemisaefolia*, was collected at Syracuse, New York. The material of *A. candida* on *Bursa* was collected at Columbus, Ohio. All the material was fixed in chrom-acetic killing fluid and imbedded in paraffin in the usual way. The methods in general were the same as those employed in the study of *A. Bliti*, and are described in detail in Bot. Gaz. **28** : 233. 1899. The Flemming triple stain was used throughout, and I am convinced that it is best for the study of Albugo, although it is exceedingly sensitive to manipulation, and the different species of Albugo require quite different treatment.

The results of this investigation are presented in three sections, entitled "descriptive," "phylogeny," and "general considerations." The first section describes the phenomena observed, avoiding theoretical considerations and presenting only what may be regarded as established facts. The second section considers the phylogenetic bearing of this research. The third section considers the genus from the comparative standpoint, an attempt being made to interpret the significance of the phenomena, and to call attention to analogous phenomena in other organisms.

The species discussed were kindly determined by Dr. Paul Magnus, who assures me that the names and synonymy are as follows: Albugo Portulacae (DC.) O. Ktz. (*Uredo Portulacae* DC., *Cystopus Portulacae* Lév.); A. Tragopogonis (Pers.) S. F. Gray (*Uredo candidus Tragopogonis* Pers., *Cystopus Tragopogonis* Schröt., *Uredo Tragopogonis* DC., *Cystopus cubicus* Lév., *C. spinulosus* DBy., *Uredo cubica* Strauss); A. candida (Pers.) O. Ktz. (*Uredo candidus* Pers.).

I wish to express my chief thanks to Professor Strasburger for daily counsel during the progress of this research; to Professor Magnus for names and synonymy; to my wife for the preparation of the slides, and for Plate IV; and to the University of Chicago for the advantages derived from a traveling fellowship.

I. DESCRIPTIVE.

ALBUGO PORTULACAE.

The early stages of the sex organs in *A. Portulacae* differ in no essential detail from those described for *A. Bliti* (Stevens 1899, *figs. 42, 43, 45, 59–65*). The nuclei are distorted as the protoplasm flows into the developing oogonium, but as this structure attains its full growth and recovers its turgor they regain their spherical form and enlarge, rapidly assuming the spirem condition. They are more numerous than in any of the other species examined, ranging from 300 to 400 in each oogonium, and are smaller than in *A. Bliti*, rendering this an unfavorable type for cytological study.

The aggregation of the cytoplasm into several regions of greater density is the first indication of the development of the oosphere (*fig. 1*). The aggregations soon coalesce, forming one large mass of fine uniform cytoplasm. Apart from the structural differences between the dense alveolar center and the vacuolate filar periphery, there is a very distinct difference in stain reaction. The dense fine-grained cytoplasm refuses the gentian, but takes the orange G lightly, while the vacuolate peripheral cytoplasm takes the gentian strongly. The uniform dense alveolar region is the rudimentary oosphere, and is centrally placed in the oogonium (*fig. 3*).

Throughout this differentiating process the nuclei, which are now in mitosis, are crowded out of the denser masses and come to lie near the larger vacuoles (*fig. 2*). Therefore, after the denser masses have coalesced and the larger vacuoles are forced into the periplasm, the nuclei are to be found near the rather indefinite boundary between periplasm and ooplasm. This boundary, however, becomes distinct and sharp immediately after the nuclei have passed to the periphery. Meanwhile the mitosis advances from prophase to metaphase.

The oogonium in this condition presents typically a region of uniform finely vacuolate cytoplasm devoid of nuclei, surrounded by a zone of cytoplasm bearing large vacuoles and containing the nuclei in metaphase. This condition I have termed the stage of *zonation* (*fig. 3*). A full understanding of this stage is necessary to interpret it in other species. Zonation presents the first clear differentiation of ooplasm from periplasm at a time previous to the existence of any wall between these parts, and finds the ooplasm nearly or quite devoid of nuclei. Zonation is very definitely and clearly marked in *A. Bliti* and *A. Portulacae*, the periplasm and ooplasm being as sharply separated as though an actual wall existed between them, but is much less conspicuous in *A. Tragopogonis* and *A. candida*, thus rendering these species more difficult of interpretation.

Immediately following zonation the nuclei divide, many of them lying in such a position that one of their daughter nuclei reenters the ooplasm. In *A. Bliti* nuclei are frequently found in late anaphase with one daughter nucleus lying inside of the oosphere and the other in the periplasm, thus affording direct evidence of the derivation of the primary oospheric nuclei. This rarely occurs in *A. Portulacae*, as the dividing nuclei usually lie quite outside of the line separating ooplasm and periplasm. The results, however, are precisely those presented in *A. Bliti*, namely, one of the daughter nuclei of each mitotic figure, lying with its long axis approximately perpendicular to the boundary of the oosphere, reenters the ooplasm (*figs. 4, 5*). The resulting oosphere contains many nuclei, the number usually varying from 50 to 100 in this species.

These primary oospheric nuclei now divide mitotically, and their products function as the female sexual elements. It should be carefully noted that there are here, as in *A. Bliti*, two mitoses in the oogonium. The first occurs during the differentiation of the oosphere and provides the primary oospheric nuclei. The second occurs in the oosphere (*figs. 6, 7*) and results in the female nuclei. These two divisions may be recognized at a glance, inasmuch as the mitoses are simultaneous for all the nuclei concerned. The nuclear figure of the second mitosis differs from that of the first in that the nuclear membrane disappears and there are fewer spindle fibers. The second mitosis usually affects only those nuclei that lie in the clearly differentiated oosphere.

Peculiar activities are present in the center of the oogonium shortly before zonation, which lead to the formation of the coenocentrum. This structure, much less conspicuous and much more ephemeral in *A. Portulacae* than in *A. Bliti*, is of the same general nature, however, and needs no special description. The central globule is found only rarely and is very small.

The development of the antheridium of *A. Portulacae* is similar to that of *A. Bliti* in its general features. Simultaneously with the mitosis of the oogonium two mitotic divisions occur in the antheridium, but the difference which is so clearly apparent between the nuclear figures of the first and second mitoses in the oogonium is not found in the antheridium. The antheridial cytoplasm stains darkly with the gentian violet, and resembles the periplasm rather than the ooplasm of the oogonium. The antheridia lie closely appressed to the oogonia, and it is not unusual to find more than one adhering to the same oogonium, a condition much more rarely seen in *A. Bliti*.

A slight papilla is developed from the oogonium into the antheridium at their point of contact. This is the "receptive papilla," first described by Wager (1896) for *A. candida*, and it reaches most remarkable proportions in *A. Portulacae* (*figs. 1, 5, 6*). In its early stages it resembles the receptive papilla of *A. candida* and *A. Bliti*, being merely a slight protuberance extending from the oogonium to the antheridium.[1] In *A. Portulacae*, however, it reaches much greater proportions (*fig. 5*). Its development occurs at a later period than in the other species, usually after the differentiation of the oosphere or even during the second mitosis, while in *A. Bliti* it precedes the preliminary massing of the cytoplasm. In *A. Portulacae* the oosphere sometimes protrudes into this papilla, a phenomenon not occurring in *A. Bliti*, since its oosphere has not been differentiated when the papilla is formed. The condition presented in *fig. 6* shows that sometimes the papilla becomes ruptured. This I cannot regard as normal, however, since only one of the hundreds of preparations examined shows such a condition.

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[1] The account of the structure in *A. Bliti* (Stevens 1899) traces the growth of the papilla in detail.

The mode of formation of the antheridial tube is uncertain. In somewhat advanced stages it is found extending nearly to the center of the oosphere. It has a well-defined wall, and is firm and straight (*fig. 8*), differing from the swollen gelatinous tube of *A. Tragopogonis* and *A. candida*, but agreeing closely with that of *A. Bliti*.

In no case was the antheridial tube in a mature oogonium seen to contain less than fifteen nuclei, and in most cases there are probably 150 or more. I have seen the tubes in transverse, longitudinal, and oblique sections, and they were always multinucleate and extended into multinucleate oospheres (*figs. 7–9*). The male nuclei are oval as they lie in the end of the antheridial tube, and stain more darkly at the anterior end. Whether there is any constant numerical relation between the sperm nuclei and oospheric nuclei could not be determined with any accuracy, owing to the great number of sperm nuclei crowded into the antheridial tube. When fully developed, the antheridial tube opens as in *A. Bliti*. There is first a softening of the wall, which is probably due to the presence of an enzyme, and it is finally dissolved, allowing the nuclei to escape and pair with those of the oosphere (*figs. 10, 11*). Before fusion both male and female nuclei enlarge somewhat, although they maintain a typical resting condition during fusion and regain their original size soon after. The result is an oospore containing between 100 and 200 nuclei, which passes the winter without further change.

A very few winter spores were seen with a relatively small number of nuclei, in one case as few as six, but this condition must be regarded as very exceptional. Such cases probably result from a fertilization of oospheres containing few female nuclei, and such are rare.

It is unnecessary to describe further the development of the spore, since its course is apparently parallel with that of *A. Bliti*. It consists simply of an accumulation of food stuffs and a growth of protective structures. A portion of a mature wall is shown in *fig. 12*. The endospore consists of one layer only, not two, as I have described in *A. Bliti*.

Berlese, in a recent paper, entitled "Ueber die Befruchtung und Entwickelung der Oosphäre bei den Peronosporeen," discusses some of the cytological phenomena of this genus. In this study he has included observations on *A. Portulacae*, giving six figures to represent the species. His results differ essentially from mine, a difference which is the more interesting since similar technique was employed, and in both cases the host plant was *Portulaca oleracea*. For the sake of clearness I will indicate some of the discrepancies between his work and my own. Berlese finds thirty to forty nuclei in an oogonium before mitosis, and says that these nuclei divide several times, the nucleoli vanishing during prophase. My preparations show 300 to 400 nuclei which divide twice, their nucleoli persisting till late anaphase. He finds ten to twelve nuclei in an antheridium, while my material shows a number several times greater. Notwithstanding his statement (p. 176), "das Cytoplasma, welches den in der Gonosphäre zurückgebliebenen Kern umgiebt, ist dicht und sehr fein gekörnt," the ooplasm which he represents is much more coarsely vacuolate (Berlese, 1898, *figs. 2–4*) than in any Albugo I have examined. Indeed, it does not resemble the ooplasm of a typical Albugo, which varies but little, so far as my observation goes, but rather presents the features of the ooplasm of Peronospora. He notes no "receptive papilla," and the antheridial tube in both structure and content is very unlike that described in this paper. He describes the chromosomes as visible in the male nucleus during fusion (p. 179), and counts them. None of the species I have examined presents a possibility of counting chromosomes at this stage, inasmuch as the nuclei fuse in typical resting condition, and the chromosomes are then absolutely indistinguishable. Many other discrepancies might be enumerated.

Such marked divergences, aside from the fact that Berlese has described a uninucleate oosphere and antheridial tube, while I find them both clearly multinucleate, are sufficient to warrant the suspicion that we are working with quite different species. Still, only one species is as yet described on *Portulaca oleracea*, and the configuration of the spore wall represented and described by Berlese agrees fully with that of the form discussed in this paper.

I have taken particular care to convince myself of the identity of the species used, and have the assurance of Professor Magnus that my species is truly *Albugo Portulacae*. Furthermore, I have been able to compare this material with authentic European herbarium specimens, and they agree precisely. Not only do my preparations agree with European material in gross characters, but the cytoplasmic structures agree with those carefully figured by Istvánffi (1895, *pl. 36, figs. 24, 25*). This agreement emphasizes the identity of the American with the European species, and further shows that the species from widely separated regions[2] do not vary appreciably even in the cytoplasmic phenomena regarding which Berlese and I report such diametrically opposed observations.

It is difficult to explain these numerous and serious discrepancies. Great variation in cytological detail is to be expected in this genus, and possibly the Italian form differs from the American as well as from that which Istvánffi studied. This is improbable, however, in view of the close agreement between these two latter forms. The problem can hardly find definite solution until the Italian form has been studied more closely. A mere difference in the number of functional nuclei, even a difference so great as that between the multinucleate and uninucleate oosphere, is readily conceivable in the same species when the condition presented by *A. Tragopogonis* is borne in mind. Berlese, however, describes no such phenomena as are seen in *A. Tragopogonis,* nor does he see the coenocentrum. Thus it appears that in the Italian form the reduction to a uninucleate condition, if such a condition really exists, is of an entirely different nature from that described in this paper.

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[2] I have been unable to learn where Istvánffi collected his material, but assume that it is of European origin.

ALBUGO TRAGOPOGONIS.

In *A. Tragopogonis* there is a simple fertilization. One male nucleus is conveyed into the oosphere, where it fuses with one oospheric nucleus. To understand the variation between this form of fertilization, also characteristic of *A. candida,* and that shown by *A. Bliti* and *A. Portulacae,* it is necessary to follow carefully the stages in the development of the oosphere in the two former species, and to homologize them with those presented by the two latter.

In *A. Tragopogonis* the oogonium and oospore are smaller than in *A. Bliti* or in *A. Portulacae.* The number of nuclei is less in proportion to the size of the oogonium, however, so that for each nucleus there is more available space. This obviates much of the dense crowding of mitotic figures seen in *A. Bliti* and in *A. Portulacae* at the time of zonation, rendering this a favorable type for study. The small size of the oosphere, however, makes it much more difficult to recognize the stages of development, so that even the preliminary examination must be made under an immersion lens.

The early stages are similar to those described for *A. Portulacae.* The protoplasm flows into the oogonium, the nuclei enlarge, the cytoplasm masses in the center, and finally the fully developed stage of zonation is reached. As in *A. Bliti* and *A. Portulacae,* this is a well-marked developmental stage (compare *figs. 28* and *3*), although it does not stand out with quite the clearness that obtains in those species. There is one central area of dense fine-meshed alveolar ooplasm, which is very clearly differentiated from the filar deeply staining periplasm. The central region, which at this time contains a very prominent coenocentrum, is entirely devoid of nuclei. They surround the central region, lying wholly within the periplasm, and are usually in metaphase. In this species, as in *A. Portulacae*, the mitosis is nearly completed in the periplasm, and the daughter nuclei do not begin to push back into the ooplasm until the chromosomes have retreated from the equatorial region of the spindle. It is also apparent that only those nuclear figures which are appropriately oriented contribute daughter nuclei to the ooplasm, and that only one of the pair gains entrance. From their mode of entrance it follows, as in *A. Portulacae*, that the chromatic content of the nuclei is situated at the end most distant from the sister nucleus. The nuclei number about fifty, and the tendency toward lowering the number that is occasionally seen in *A. Portulacae* is not apparent here.

The primary oospheric nuclei now undergo a second mitosis, which is clearly distinguishable from the first by the character of the chromatic figure, which is similar to that described for *A. Portulacae*. The fact that the second mitosis involves only the oospheric, not the periplasmic nuclei also distinguishes it from the first (*figs. 32, 34*).

The definiteness with which ooplasm and periplasm are delimited at and after zonation (*figs. 28–31*) precludes any possibility of confounding pre- and post-zonation stages. The clearness of the nuclei, which are seen as they enter the oosphere (*fig. 29*), and which can be followed through all the stages of the second mitosis (*figs. 32, 34*), renders it equally certain that in *A. Tragopogonis* the oosphere is multinucleate. So far there has been no deviation from the course followed by *A. Bliti* and *A. Portulacae*.

These potential female nuclei appear to differ from each other in no important respect, unless it be in their distance from the coenocentrum, yet under the usual conditions only one of them is destined to function as a sexual nucleus. A study of later stages shows that one (or very rarely two or three) of these nuclei comes to lie in close contact with the coenocentrum, and there grows (*figs. 35–37*) until it becomes many times its former size and much larger than the nuclei found at earlier stages in the developing oosphere.

A study of oospheres after the second division shows the potential female nuclei in various stages of degeneration. They appear first to lose their chromatin network, the nucleoli and membrane persisting longest. Such degenerate nuclei can be found in abundance in the stages indicated. Frequently one or two rather large and apparently normal nuclei are found in an oosphere, which also has its one large nucleus in contact with the coenocentrum. In other cases, many very small nuclei are to be found in the ooplasm, and one large nucleus near the coenocentrum. These small nuclei range from the normal size to such small dimensions that only the nucleolus can be perceived with certainty. It would be impossible to recognize the smallest as nuclei, were it not that they are connected with undoubted nuclei by a series of complete gradations, and from the fact also that they lie in a cytoplasm remarkably clear and free from granules. Occasionally these extremely small nuclei are found in mitosis. Sometimes I have found groups of supernumerary nuclei, and often small ones are found in pairs, as though trying to fuse (*fig. 38*). Since this condition has never been found before the opening of the antheridial tube, it may represent the pairing of a supernumerary oospheric with a degenerate antheridial nucleus.

That these inclusions described as degenerate nuclei are really nuclei is established by their structure and behavior. That they do not result from the division of a fusion nucleus is shown by their presence when the male and female nuclei are found lying together, but still unfused in the same oosphere (*fig. 38*). The degenerate nuclei, as would be expected, are most numerous immediately after the second mitosis, while the one functional nucleus which lies near the coenocentrum is yet small. Before the opening of the antheridial tube nearly all have disappeared. There is convincing evidence that the oosphere is at first multinucleate (*figs. 30–32, 34*) and eventually uninucleate (*fig. 36*). There is no evidence to indicate that any nuclei escape through the boundary into the periplasm, but they are seen in the ooplasm in all stages of degeneration.

The coenocentrum in *A. Tragopogonis*, as in *A. Bliti* and *A. Portulacae*, makes its appearance when the central mass of ooplasm is formed just before zonation (*figs. 27, 28*). It first consists of an area of cytoplasm which takes the orange G with great avidity, while the neighboring cytoplasm stains deeply with the gentian violet. A trifle later than zonation the coenocentrum is very highly developed, and appears in section as several zones of cytoplasm differing in density and stain reaction. The innermost area is coarsely vacuolate, and stains lightly with orange G. This region is surrounded by a narrower zone of dense granular cytoplasm, which is in turn encompassed by a less dense zone, and this finally by a broad zone of cytoplasm which stains more deeply with gentian violet. This condition is not greatly changed at the time of entrance of the primary oospheric nuclei represented in *fig. 30*. In later stages the outer zones are lost, and the innermost region assumes a characteristic homogeneous oily appearance and is quite spherical (*fig. 31*). About the time of the second mitosis the innermost region, all that remains of the coenocentrum, loses its clear appearance and becomes coarsely granular (*fig. 32*), and in its stain reaction shows the probability of nuclear contents. The vacuolate area seen in the center of very young coenocentra (*fig. 30*) is probably a reservoir for the reception of foods that are elaborated by the surrounding (presumably zymogenic) zone, which is in turn encompassed by typical trophoplasm. As the coenocentrum becomes older, these vacuoles, or rather globules of food stuffs in the protoplasm coalesce, and form the one central globule, which at first has a clear oily appearance (*fig. 31*), although it is not a true oil.

The coenocentrum possesses an attraction for the nuclei similar to that noted by Wager (1900) in *Peronospora parasitica.* Nuclei in greatly elongated condition, apparently moving toward the coenocentrum, give sufficient evidence of this (*figs. 30, 31*). As a result, several nuclei come into actual contact with and even penetrate the coenocentrum (*figs. 32, 34*), and are thus found during all stages of the second mitosis. In some cases only one nucleus in mitosis is found thus attached; in others as many as three seemed to be so anchored, and probably, if the sphere could be viewed from all sides, as many as six or seven nuclei could be seen attached to the coenocentrum. The other primary oospheric nuclei are found lying free in the neighboring ooplasm in a similar stage of mitosis. It is not probable that any nuclei actually enter the coenocentrum, inasmuch as it maintains its homogeneous appearance until considerably later.

After the completion of the second mitosis, one small nucleus is found lying very close to the coenocentrum, possibly attached to it, although the evidence in *A. Tragopogonis* is not clear. Older stages show a larger nucleus. As the size of the nucleus increases, the coenocentrum becomes more granular (*figs. 35-37*), and loses its definite form, eventually appearing simply as a granular mass partially enveloping the female nucleus. As has been said, there is usually only one nucleus lying beside the coenocentrum after the completion of the second division, although several are in contact with it during this process. The oosphere when ready for fertilization contains one large nucleus which lies beside the remains of the coenocentrum. A few small degenerating nuclei, frequently present, are scattered throughout the ooplasm, which still maintains that fine-meshed alveolar structure that characterizes it after zonation.

Few phenomena of interest were observed in connection with the entrance of the antheridial tube. It has a much thinner wall, and is of more gelatinous nature, than that of *A. Bliti* or of *A. Portulacae*, and disappears more quickly after discharging its contents. It usually bears several degenerate nuclei as well as one or two that are larger and apparently capable of functioning. *Fig. 33* shows an unopened tube which contains a greater number, although in this case the oosphere clearly possessed only one functional nucleus. The rupture of the tube, accompanied by the discharge of its contents, may occur at some distance from the female nucleus or nearly in contact with it. When the sperm nucleus is liberated it assumes an oval shape as it migrates toward the female (*fig. 36*).

The male is much the smaller when the nuclei first come in contact, although at this time it is larger than an ordinary vegetative nucleus. Fusion does not occur at once, but the nuclei lie together, imbedded in the remains of the coenocentrum. This period of rest must be of considerable duration, since the stage is found in great abundance, and the oosphere wall develops perceptibly at this time. During this period of quiescence the male nucleus enlarges until it eventually equals the female in size (*figs. 37, 38*) or nearly so. Fusion then occurs, both nuclei being in resting condition. An increase in the number of degenerating nuclei occurs in the oosphere simultaneously with the opening of the antheridial tube. This is quite evidently due to supernumerary antheridial nuclei which are clearly introduced (*fig. 33*). These nuclei, although some of them appear perfectly normal, at length degenerate and eventually dissolve, since only one nucleus is to be found when the fusion is complete. There is no evidence of a general fusion such as is described by Hartog (1891) and Golenkin (1900). This species presents a clear case of the presence of fertilized and unfertilized nuclei in the same cytoplasm, and illustrates the inability of the unfertilized nuclei to survive these conditions.

Before the accumulation of food advances far, the fusion nucleus divides, presenting a nuclear figure which is enormous in comparison with those in the oogonium and oosphere (*fig. 40*). As these divisions succeed one another, the nuclei decrease in size, so that those of the winter spore are about the size of the vegetative nucleus, and are probably about thirty or forty in number (*fig. 41*). Wager (1896) estimated the number in *A. candida* to be thirty-two. In ripening the spore exhibits those changes in wall and contents which characterize the other members of this group.

ALBUGO CANDIDA.

The result of the study of *A. Tragopogonis* suggested that the great variation in mode of fertilization seen in this genus might be explained in a way hitherto unsuspected. I have studied *A. candida*, therefore, comparing it stage for stage with the other species referred to in this paper. My observations essentially agree with those of Wager (1896), which were confirmed and extended by the research of Davis (1900). I have here only to present some further details, to make certain homologies clear, and in no radical way to alter the statements of these two writers.

The initial step in development consists of a differentiation of the ooplasm in the center of the oogonium, the nuclei in the meantime undergoing mitosis. One stage in this process is beautifully figured by Davis (1900, *fig. 2*), and a stage slightly older is herewith presented (*fig. 14*). It should be noted in these figures that the ooplasm is much more vacuolate than in the other known species (*figs. 3, 14, 28*). Particularly in the figure by Davis will it be seen that the ooplasm is separated from the periplasm by a rather broad irregular zone of very dense cytoplasm.

The conditions presented even in this early stage of oogenesis are markedly different from those of the other species. There is apparently no preliminary aggregation of cytoplasm into masses, but rather a simultaneous movement from the oogonial wall toward the center, leaving behind only slender threads of cytoplasm. It appears as though this movement occurs as a wave starting at the oogonial wall and moving so as to crowd the cytoplasm into the dense zone represented in the figures. When this condition obtains, the nuclei are approximately in metaphase, and it is clear that this represents the first nuclear division. Nuclei in metaphase and late anaphase may be seen in the same oogonium, but it is not probable that one nucleus undergoes more divisions than another, since the nuclei simultaneously pass through the stages of early prophase.

At a somewhat later stage, judging by the development of the coenocentrum, the zone of dense cytoplasm represented in *fig. 14* (Davis 1900, *fig. 2*) disappears. The rudimentary oosphere consists then of uniformly distributed cytoplasm, together with the nuclei which have completed their mitoses (*fig. 15*). This condition is characterized by the well-developed coenocentrum, the presence of nuclei which are not in mitosis, and the central mass of dense, uniform, deeply staining cytoplasm which is suspended from the oogonial wall by delicate threads. Some of the nuclei now enter a second mitosis, and these may be found in various stages lying in this clearly marked central region. Those lying outside in the periplasmic region do not divide again, a distinction which is maintained in all species of Albugo.

Before the inception of this second mitosis, during its progress, or after its completion, the nuclei pass toward the periplasm (*figs. 15–17*) until all but one has left the ooplasm. The plasmoderma[3] is now formed, preceded by the first sharp differentiation of ooplasm from periplasm. This is immediately followed by the wall, a condition illustrated by Davis (1900, *fig. 4b*).

What stage in *A. candida* corresponds to zonation in the other species? Is it the stage represented by *fig. 14*, where the ooplasm is bounded by a dense layer of protoplasm; or later (*fig. 15*) when the oosphere is somewhat more sharply differentiated; or still later when the nuclei have left the central region and the plasmoderma is about to be formed? The stage shown in *fig. 14* has nothing in common with zonation except that the nuclei are in metaphase of the first mitosis. Zonation is chiefly characterized by that sharp differentiation of ooplasm and periplasm which precedes the plasmoderma. This character is absent here, as well as from the stage represented in *fig. 15*. A distinct differentiation does not obtain until all of the superfluous nuclei have left the ooplasm (Davis 1900, *fig. 3*). This is clearly the stage nearest to zonation in character, therefore, although it differs much from the zonation of the other species in general appearance. The absence ot preliminary protoplasmic aggregation precludes the early marshaling of the nuclei into the form of a hollow sphere, a phenomenon which is so characteristic of the zonation stage in *A. Bliti*, *A. Portulacae*, and *A. Tragopogonis*. It may be for this reason, also, that the formation of the plasmoderma is delayed.

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[3] The term *plasmoderma* has been suggested to me by Professor Strasburger as a desirable equivalent for the much-abused *Hautschicht*, which was originally intended for purely German usage. From its relation to cell activities (Noll 1888) and its characteristic kinoplasmic content the plasmoderma is to be regarded as a structure quite distinct from that designated by the term *ectoplast*.

The mode of development of the coenocentrum and its relation to the oospheric nuclei remain to be considered. The coenocentrum was first observed by Wager (1896) in *A. candida*, and its development has been more closely followed in the same species by Davis (1900). The structure was given its present name, and its nature and history were discussed to some extent, in my earlier paper on *A. Bliti* (1899). Wager (1900) further notes its presence in *Peronospora parasitica*, and observes that it has there an attraction for the one reentering female nucleus. I have already called attention to the same phenomenon in *A. Tragopogonis*. This attraction is strikingly exhibited in *A. candida*, and demands a somewhat detailed consideration.

A very early stage in development is shown by Davis (1900, *fig. 2*.) In a later stage the coenocentrum contracts, and a large globule appears at its center, much as in *A. Tragopogonis*, with the exception that the coenocentrum is very granular. The granules resemble the nucleoli of this species, both in size and stain reaction. They appear to enter the coenocentrum from the ooplasm in very early stages, and may be seen in great numbers in the adjacent region (*fig. 13*). The nuclei at this period are in mitosis, and it is quite usual to see two, three, or more spindles lying with one apex imbedded in the coenocentrum (*figs. 16, 18–20*). Their form is elongated before their attachment, and it is evident that the coenocentrum possesses an attractive influence. A similar attraction has been observed in *Peronospora parasitica* (Wager 1900) for resting nuclei, and by myself in *A. Tragopogonis;* but the phenomenon of attraction is exhibited in *A. candida* during mitosis. It often results in a spindle nearly twice the normal length and proportionately narrower. Such cases are represented in *figs. 18–20*. The consequence of mitosis under these conditions is that several daughter nuclei remain anchored to the coenocentrum (*figs. 17, 21, 22*). Whether there is an organic attachment or merely an imbedding of a projection is impossible to say, but certainly these daughter nuclei protrude a long pseudopodium-like extension which penetrates the coenocentrum to a considerable depth. In late stages, as the nuclei pass to the periplasm, fewer are found attached to the coenocentrum, with the result that eventually only one remains. This nucleus enlarges greatly, and is often found lying in the cytoplasm in such a position as to suggest that it had been fixed while swaying to and fro on the stalk-like pseudopodium which attaches it to the coenocentrum. The migration and attachment of the nuclei to the coenocentrum seem inexplicable on any basis save that of chemotactic influence.

The growth of the nucleus while in contact with this structure, both in this species and in *A. Tragopogonis*, gives evidence that the coenocentrum functions as an organ of nutrition for the one surviving nucleus. In some respects the coenocentrum resembles a trophoplast, but the presence of granules, probably of kinoplasmic nature, renders the analogy less complete. It seems also to arise *de novo* in each oogonium, a character not in agreement with the theories most generally accepted. The evidence that such structures always arise from preexisting ones is not conclusive, however, and the work of Davis (1899) on Anthoceros may indicate that the chloroplast in that plant arises *de novo* in each sporophyte from the cytoplasm of the spore mother cells, although the author does not definitely draw that conclusion. If such be the case, the similarity between the coenocentrum and the chloroplast is closer. Evidence of high specialization in chloroplasts is given, moreover, in observations of Oltmanns on Coleochaete (1898), and of Davis on Anthoceros (1899), where the chloroplasts divide in advance of the nuclei, so as to provide daughter structures equal in number to the nuclei which are to be formed. Considering the coenocentrum as a source of nutrition, the phenomenon of chemotaxis here as affecting the position of the nuclei is quite parallel to that exhibited so abundantly in animal cells, where the nuclei wander toward the source of nutritive supply (Korschelt 1889). The development of the pseudopodium-like structure also has its analogy in the animal cell, where the nucleus becomes amœboid or protrudes many pseudopodia in order to enlarge its absorptive surface (Korschelt 1889). In the nucleus under consideration the nature of the nutriment may render it more advantageous to penetrate by means of one sharp projection. While many plants possess cells having very irregularly shaped nuclei, *e. g.*, endosperm cells of Zea, epidermal cells of Allium, Hyacinthus (Zimmermann 1896), amœboid movements are much more rare in plants than in animals. Kohl (1897) by the action of asparagin has incited such movements in the nuclei of the cells of Elodea and Tradescantia, and considers them comparable with the phenomena observed by Korschelt (1889). This also throws light on the behavior of the nuclei in Albugo. Kohl considers with Korschelt that the amœboid movement stands in direct relation to the heightened exchange between nucleus and cytoplasm.

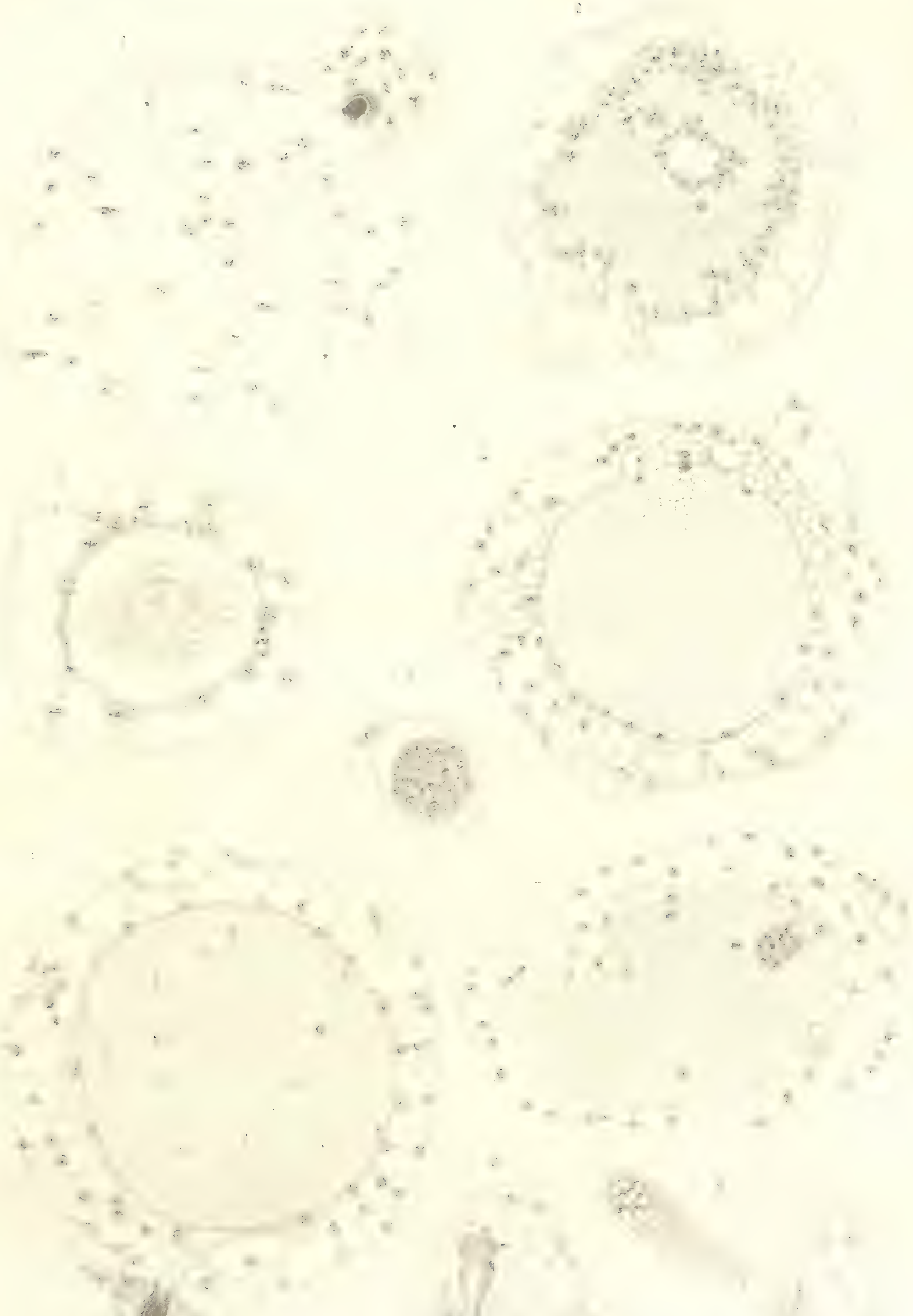
The coenocentrum may in a sense be likened to some of the so-called yolk nuclei, or *Dotterkern* of animal eggs. In *A. Bliti* (Stevens 1899, *fig. 69*) and in *A. candida* (Davis 1900, *fig. 2*) there is slight indication of radiate structure which somewhat resembles the figures of Munson (1898) illustrating the yolk nucleus of Limulus. The structures agree in having nutritive functions. In certain cases, as in Limulus and the newt (Jordon 1893), the yolk nuclei seem to develop directly from the cytoplasm, and in this further resemble the coenocentrum. A comparison of these structures emphasizes the fact that protoplasm in diverse organisms under certain conditions may become similarly differentiated for the performance of particular functions.

Concerning the antheridial tube there is but little to add.

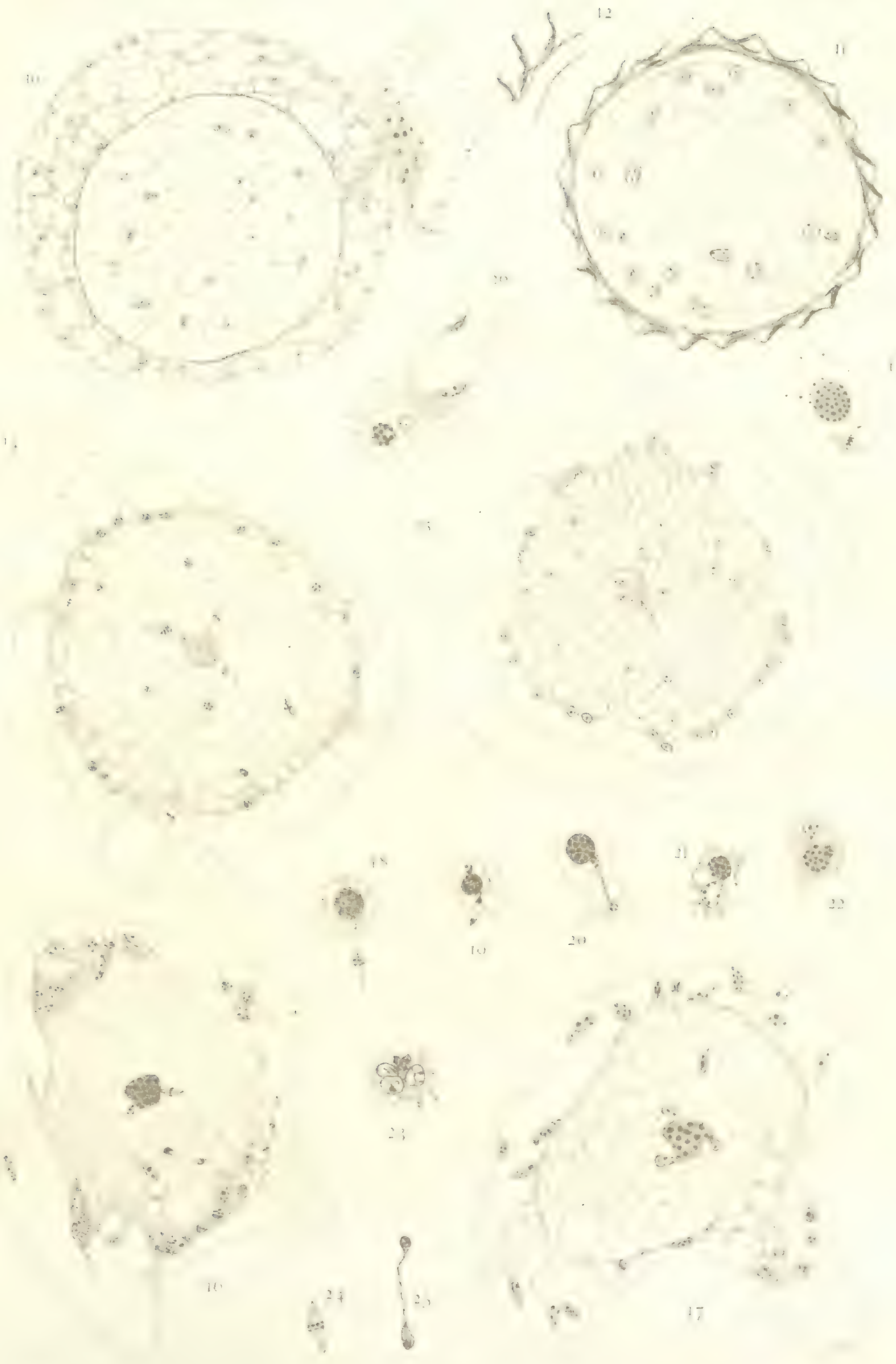
Both Wager (1896) and Davis (1900) assert that it bears one functional nucleus, but they figure other nuclei in the neck of the tube, and Davis suggests that occasionally more than one nucleus from the antheridium may enter the ooplasm. *Fig. 26* shows a case where the tube clearly contains one large male nucleus in a mass of dense cytoplasm, and another nucleus lying in such a position that it must be set free were the tube to open. It is also common to find more than two nuclei in the oosphere just after the opening of the tube and before fusion. In such cases it is evident that there is a supernumerary nucleus, but whether it is derived from the antheridium or the oosphere is not always plain. Such conditions as those shown in *fig. 17* render it probable that sometimes two or even more female nuclei might survive. The supernumerary nuclei would then be found near the coenocentrum (*fig. 23*). Occasionally the one supernumerary nucleus lies free in the ooplasm at a considerable distance from the coenocentrum, and is probably of antheridial origin. It is quite conceivable, and it may occasionally happen, that two functional nuclei are derived from each organ, and that a multiple fusion of nuclei may occur even in *A. candida*.

Figs. 24 and *25* represent two stages in the division of the fusion nucleus. The strongly thickened fibers and their contorted condition agree well with the view of Drüner (1895) that the spindle poles are separated by a push due to an elongation of the spindle, not by a pull from a region external to the nucleus, nor by cytoplasmic streaming. The division is of quite the same type as that exhibited before fusion, an agreement that is particularly evident in anaphase, so characteristic in both this and other species.

A fuller study of the species has developed one essential point somewhat at variance with previous observations. I believe I have shown that there is no time when the central region in *A. candida* is entirely devoid of nuclei, and that very early there is an attractive force exhibited by the coenocentrum which results in a retention of one nucleus while the others are



ALBUGO PORTULACAE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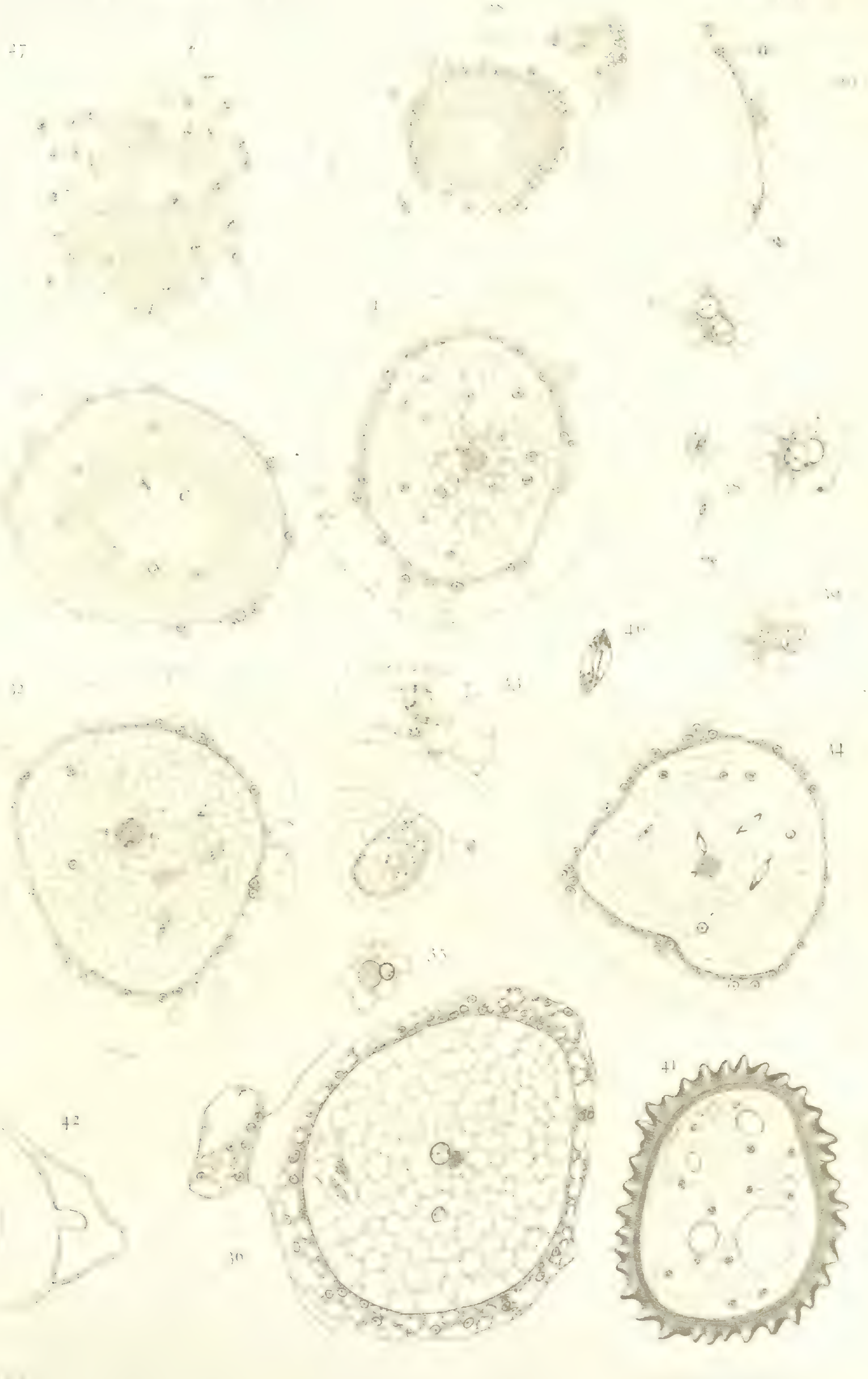
ALBUGO CANDIDA.

Lith. Anst. v. E. A. Funke, Leipzig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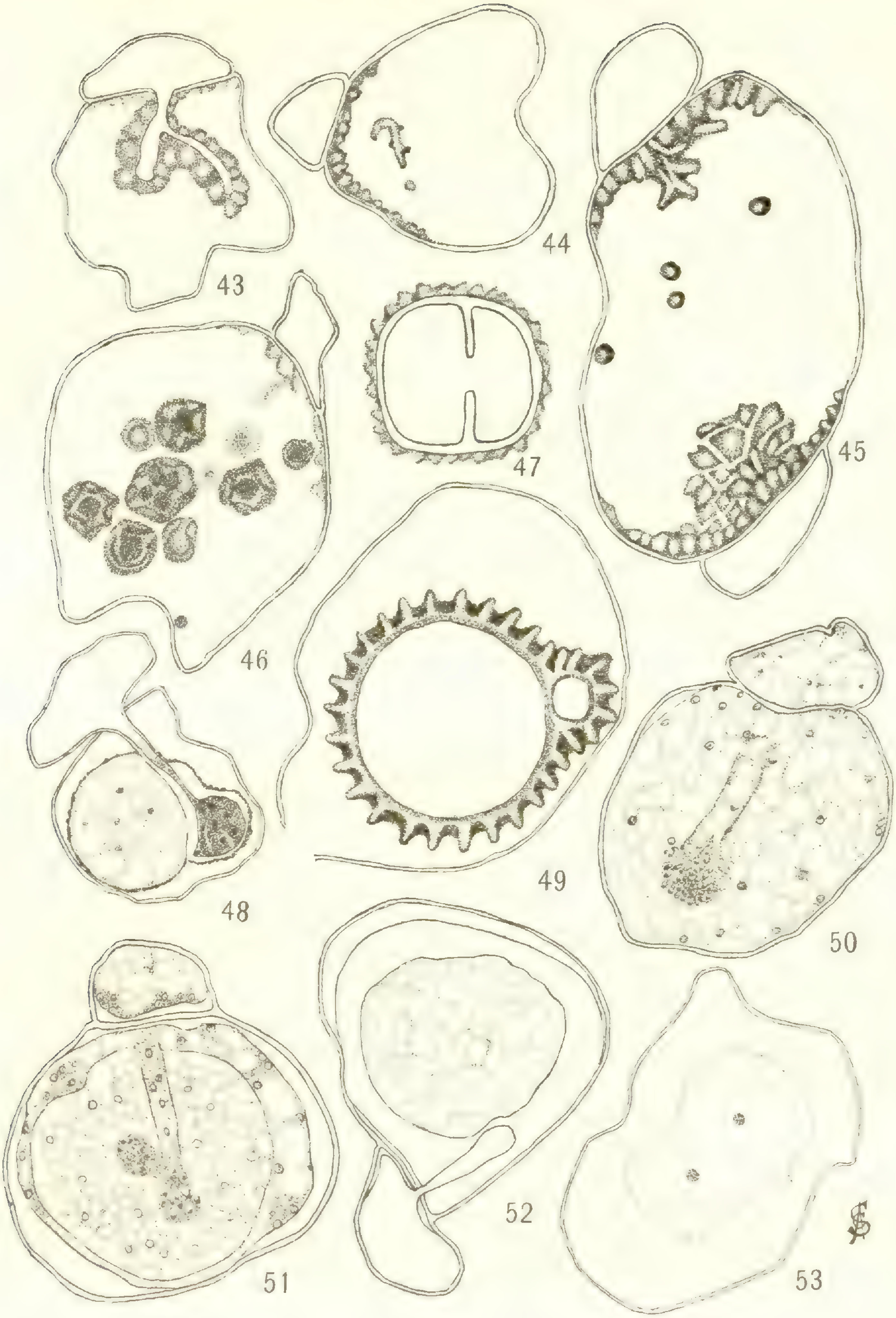
ALBUGO TRAGOPOGONIS.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STEVENS on ALBUGO

carried outside of the region of the oosphere. In this respect *A. candida* differs from the other species of Albugo.

SUMMARY.

Albugo Portulacae.

1. *A. Portulacae* possesses a multinucleate oosphere which develops in a manner very similar to that of *A. Bliti* (Stevens 1899), *i. e.*, the nuclei all pass to the periplasm, dividing mitotically; and some of the daughter nuclei reenter the ooplasm, divide again, their products becoming the female nuclei, the plasmoderma being differentiated in the meantime.

2. Two mitoses occur in both oogenesis and spermatogenesis.

3. The nuclei return to the ooplasm after division much diminished in achromatic content.

4. The nuclear figure of the second mitosis is clearly distinguishable from the first by the diminished kinoplasm.

5. The antheridial tube is multinucleate.

6. The numerous antheridial nuclei fuse in pairs with the numerous oospheric nuclei, the number of fusion nuclei being usually larger than in *A. Bliti.* These fusion nuclei pass the winter without further change.

7. A coenocentrum somewhat less highly developed than that of *A. Bliti* is present.

8. The receptive papilla in *A. Portulacae* is larger than in the other known species.

Albugo Tragopogonis.

9. A multinucleate oosphere develops in the same manner as in *A. Bliti* and *A. Portulacae*, and is then reduced to a uninucleate condition by disorganization of the supernumerary nuclei.

10. The nuclei pass to the periplasm, divide, and return to the ooplasm much diminished in achromatic content.

11. Two mitoses occur in oogenesis and spermatogenesis.

12. The nuclear figure of the second division may be distinguished from the first by a diminution of kinoplasm.

13. The antheridial tube conveys one or more nuclei into the oosphere where one fuses with the female nucleus.

14. Supernumerary male nuclei disorganize as do the supernumerary female nuclei.

15. The fusion nucleus undergoes repeated mitoses, and the winter oospore is consequently multinucleate.

16. The coenocentrum is very highly developed. It possesses an attraction for the primary oospheric nuclei and serves as a source of nourishment for the surviving female nucleus.

Albugo candida.

17. The oosphere is developed in a manner quite different from that seen in *A. Bliti*, *A. Portulacae*, and *A. Tragopogonis*. The periplasm and ooplasm are not differentiated until the second mitosis is completed. The nuclei, excepting one, eventually pass to the periplasm, which is then cut off by a wall.

18. One nucleus remains in the oosphere attached to the coenocentrum.

19. The coenocentrum attracts the nuclei very strongly, and later serves as a source of nourishment for the surviving female nucleus.

20. The antheridial tube occasionally contains two nuclei.

[*To be continued.*]

BOTANICAL INSTITUTE, BONN.

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX.

WILLIAM L. BRAY.

(WITH TWENTY-FOUR TEXT FIGURES)

WESTERN Texas has been a choice field for botanists from the earliest days, always having been accessible through the numerous army posts and government surveys. For this reason the flora early became fairly well known through numerous contributions describing the country and its vegetation, and from descriptions of species, culminating in the *Botany of Western Texas* by Professor Coulter. Since that time, the study of plants in their natural environments has enriched botanical thought, and it seems opportune to take up again the flora of western Texas and to apply to it the new methods.

A further reason for presenting the plant life of Texas as the product of its environment lies in the growing tendency to rely upon such study to furnish a rational basis for the exploitation of plant life in agriculture, horticulture, forestry, agrostology, and various other economic fields. The great diversities of climatic factors, of soils, and of physiographic conditions in the Texas region make it necessary to find the results of these factors as recorded in plants already occupying the field, that they may serve as a guide in attempting to introduce new ones. The statement that the flora of western Texas early came to be fairly well known is true only of pteridophytes and spermatophytes, for the bryophytes and thallophytes have scarcely been noticed thus far.

The present paper aims only to clear the field a little, preparatory to its cultivation along special lines; and because it is a very large field, with much to be done, it offers a strong invitation to colaborers. There is no special reason for excluding eastern Texas from this discussion, other than that the whole field is too large for a single paper. During a residence of more than three years, the writer has personally explored a great deal of the state, and yet there are vast areas he has not seen, and of which he cannot speak from first-hand knowledge. Hence even this general analysis of the vegetation must contain inaccuracies and misjudgments, which only a detailed survey of the provinces concerned will correct.

With the opportune appearance of Professor Hill's *Physical geography of the Texas region*[1] the task of presenting the climatic and especially the physiographic and geological factors has been much lightened, and by his courtesy a very free use has been made of this Texas folio. He has given much help also in the way of suggestions and photographs, which is herewith gratefully acknowledged. Dr. V. Havard's *Report of the botany of southern and western Texas*[2] has also been of great service.

The order followed is to discuss first the climatic factors in their relation to the vegetation of the region, and second the vegetation itself under several general types of association (plant formations), together with the factors of geology, soils, and physiography (edaphic factors), which determine chiefly the type of formation upon any given area. Omitting from consideration practically all of the Texas region lying to the east of meridian 97°30′, we have to deal with an area covering in its greatest north-south dimensions 10.5° of latitude (from about 26° to 36.5°), a fact of no small significance in climatic zones; and in its east-west extent 9° (from 97.5° to 106.5°), a distance sufficient to carry the western border into the Pacific zone.

CLIMATIC AND EDAPHIC FACTORS.

TEMPERATURE.

In the facts that the southernmost point of Texas is at sea level and borders on the Gulf, and is but 26° north of the equator;

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[1] U. S. Geological Survey. Texas folio. 1900.

[2] Proc. U. S. Nat. Mus. **8**:—. 1885.

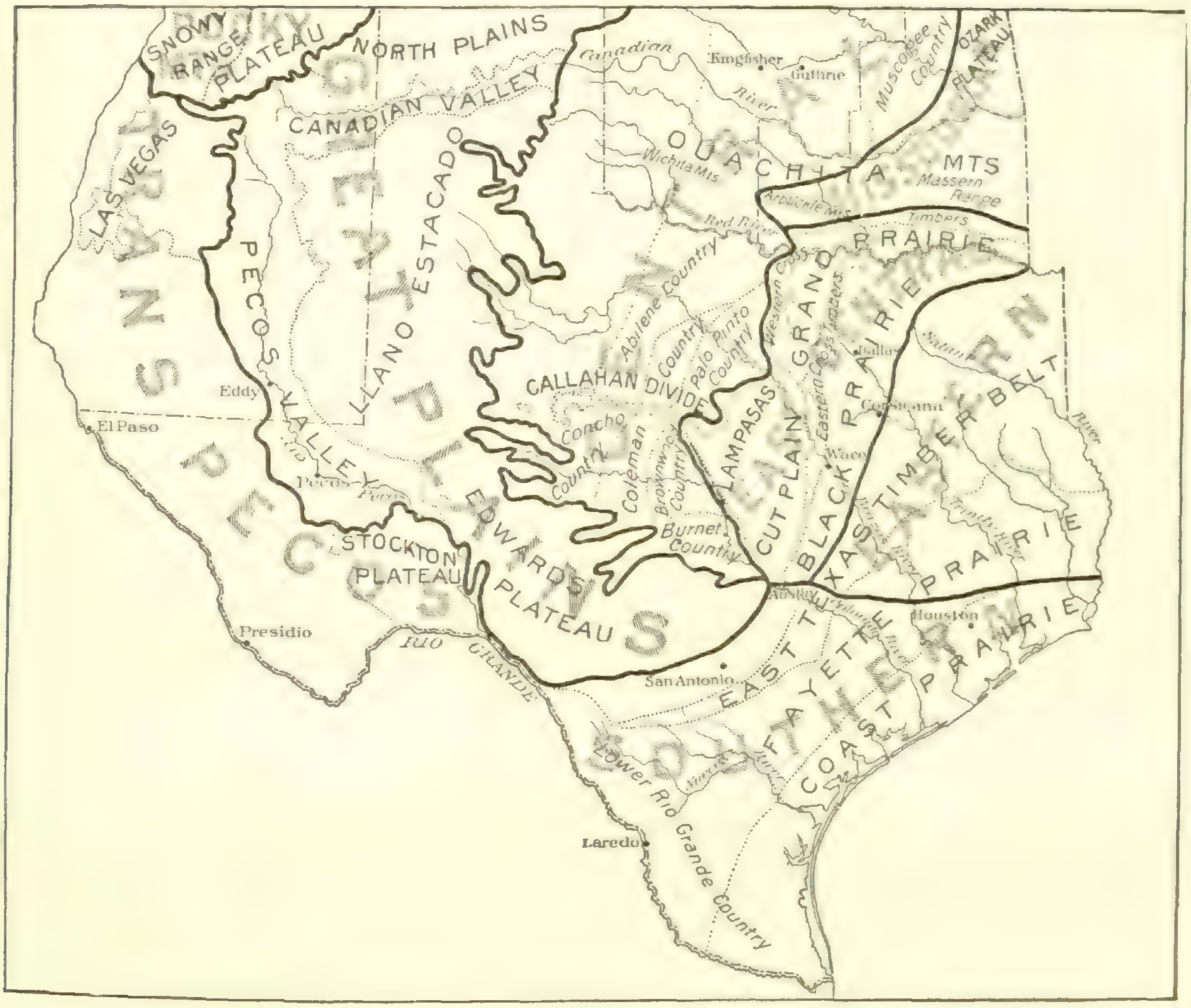
SNOWY RANGE
ROCKY PLATEAU
NORTH PLAINS
CANADIAN VALLEY
LAS VEGAS
PECOS VALLEY
LLANO ESTACADO
GREAT PLAINS
TRANS PECOS
Canadian
Kingfisher
Guthrie
River
Muscogee Country
OZARK PLATEAU
OUACHITA MTS
Wichita Mts
Massern Range
Arbuckle Mts
Red River
Timbers
PRAIRIE
Western Cross Timbers
GRAND PRAIRIE
Eastern Cross Timbers
Dallas
Sabine
Abilene Country
Palo Pinto Country
CALLAHAN DIVIDE
Eddy
El Paso
Pecos
Concho Country
Coleman
Brownwood Country
Burnet Country
LAMPASAS CUT PLAIN
BLACK PRAIRIE
Corsicana
Waco
EAST TEXAS TIMBER BELT
Trinity River
PRAIRIE
STOCKTON PLATEAU
EDWARDS PLATEAU
Austin
Presidio
RIO GRANDE
Houston
San Antonio
FAYETTE PRAIRIE
COAST PRAIRIE
SOUTHERN
Lower Rio Grande Country
Laredo
River

FIG. 1.—Physiographic provinces and minor subdivisions of the greater Texas region.—From Hill's Phys. Geog. Texas.

that the northernmost part is 10.5° removed from this, is at an elevation of 5000 feet, and directly exposed to the extremes of continental climate; and that in the latitude of 32° a mountain mass reaches the height of 9000 feet; we have an indication of the range of annual temperature for the region under discussion. The temperature conditions of the lower Rio Grande valley from October to April are about the same as those of the middle third of the Florida peninsula. Those of the Staked plains above 4000 feet are about the same as those of the southern half of Kansas, Missouri, and Illinois. Again, the daily extremes, which are reflected in the structure of species, stand out most significantly in a comparison of two extreme points. The greatest daily fluctuation at Galveston is 5 to 7°F. in April; at El Paso 25 to 27° in June–July. During the February norther of 1899, points on the Staked plains above 4000 feet registered more than 20° below zero, and it was 12° above at Brownsville on the same date. These figures indicate the extremes which may occur to bring about a periodic reduction of the Austral flora. The following temperature zones as measured by the flora prevail in the western Texas region.

DILUTE XEROPHYTIC TROPICAL.—This can be recognized only in the extreme southern part of the Rio Grande embayment, especially in the present Rio Grande valley. The mean annual temperature of the valley, however, from Laredo to the mouth, is 73°, slightly below that of southern Florida. The monthly means correspond to those of the middle part of the Florida peninsula from September to March, except the January mean which falls some degrees below. The summer means rise much higher than in any part of Florida. A record of sixteen years at Brownsville showed a minimum temperature of 18° (the minimum in February 1899 was 12°) and five years without frost. At Indianola a record of fifteen years showed a minimum of 15° and four years without frost. Probably a freeze severe enough to kill tropical woody vegetation occurs in periods of ten to twelve years. The fatal temperature for tropical plants in this region is that due to the northers, which bring abnormally low temperatures suddenly, and not infrequently during the growth season. The actual poverty of a tropical flora, however, is due equally to the aridity of the region. The floral affinities of the tropical element are with the Neotropical Gulf zone, and are a part of the Tamulipan division of this zone.[3]

The following species, as illustrations, will be recognized as belonging to groups of chiefly tropical distribution, but even some of these pass into northern and southern subtropical territory: *Sabal Adansonii*, *S. Mexicana*, *Monanthochloa littoralis*,

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[3] MERRIAM, C. H.: Life zones and crop zones, p. 52.

Jatropha macrorhiza, *J. multifida*, *Janusia gracilis*, *Aspicarpa hyssopifolia*, *A. longipes*, *Galphimia angustifolia*, *Malpighia glabra*, *Amyris parvifolia*, *Helietta parvifolia*, *Schaefferia cuneifolia*, *Serjania incisa*, *S. brachycarpa*, *Urvillaea Mexicana*, *Wissadula mucronulata*, *Hermannia Texana*, *Melochia tomentosa*.

SEMITROPICAL.— The tropical elements, which are but faintly indicated even in the southernmost part of Texas, quickly merge into a semitropical zone, which is visible and persistent even to the cañons on the border of the plains region, and especially up the Rio Grande into the Great Bend and its side cañons, and in the lower Pecos cañon, and this in spite of the great preponderance of Sonoran species of the Lower Austral. The range of *Acacia Farnesiana* and *Parkinsonia aculeata* would represent fairly the area of this zone outside the Rio Grande valley. A number of the species included in genera cited for the tropical portion extend also over this area. It is further indicated by such genera as Guajacum, Mortonia, Pistacia, Peganum, Ascyrium, Persea, Myrica, Balodendron (listed by V. Bailey from Corpus Christi), Cardiospermum, Castela, Choisya, Hermannia, Ayenia, Corchorus, and Malachra.

LOWER SONORAN.—The Lower Sonoran elements so pervade the regions containing tropical and subtropical species as to be by far the dominant flora, and to constitute the characteristic formations. If the Lower Sonoran division of the Lower Austral zone be counted from the 98th meridian in Texas, it exists in several grades of purity or intensity over the following provinces, varying with differences in temperature, moisture, and soil: (1) the Rio Grande plain, especially interior to the tropical and subtropical divisions; (2) the erosion mountainous portion of the Edwards plateau; (3) the central plains of northern Texas (including the cañon of the Canadian river across the Staked plains); (4) the Staked plains below 3500 feet and the adjoining plateau prairie to the south; (5) the Toyah basin; (6) the bolson plains and mesas of trans-Pecos Texas; (7) the Stockton plateau and slopes of the Guadalupe, Davis, and other mountains at the north up to about 4000 feet, and the slopes of the Chisos and other mountains in the Great Bend up to 6000 feet.

Of these several provinces, each of which possesses distinctive floral or physiological conditions, the Rio Grande plain is clearly related to the tropical and the subtropical in its preponderance of Mimoseae and Caesalpineae, of Rhamneae, Zygophyllaceae, Rutaceae, Simarubaceae, Malvaceae, Euphorbiaceae, Nyctaginaceae, and similar groups. The central plains of the north, on the contrary, possess a minimum of these groups, but more which are peculiar or common to the central prairie plains of Kansas, Missouri, Indian Territory, and Oklahoma, such as Compositae (certain subfamilies), Papilionaceae, Onagraceae, and others. The identity of plant formations, however, as

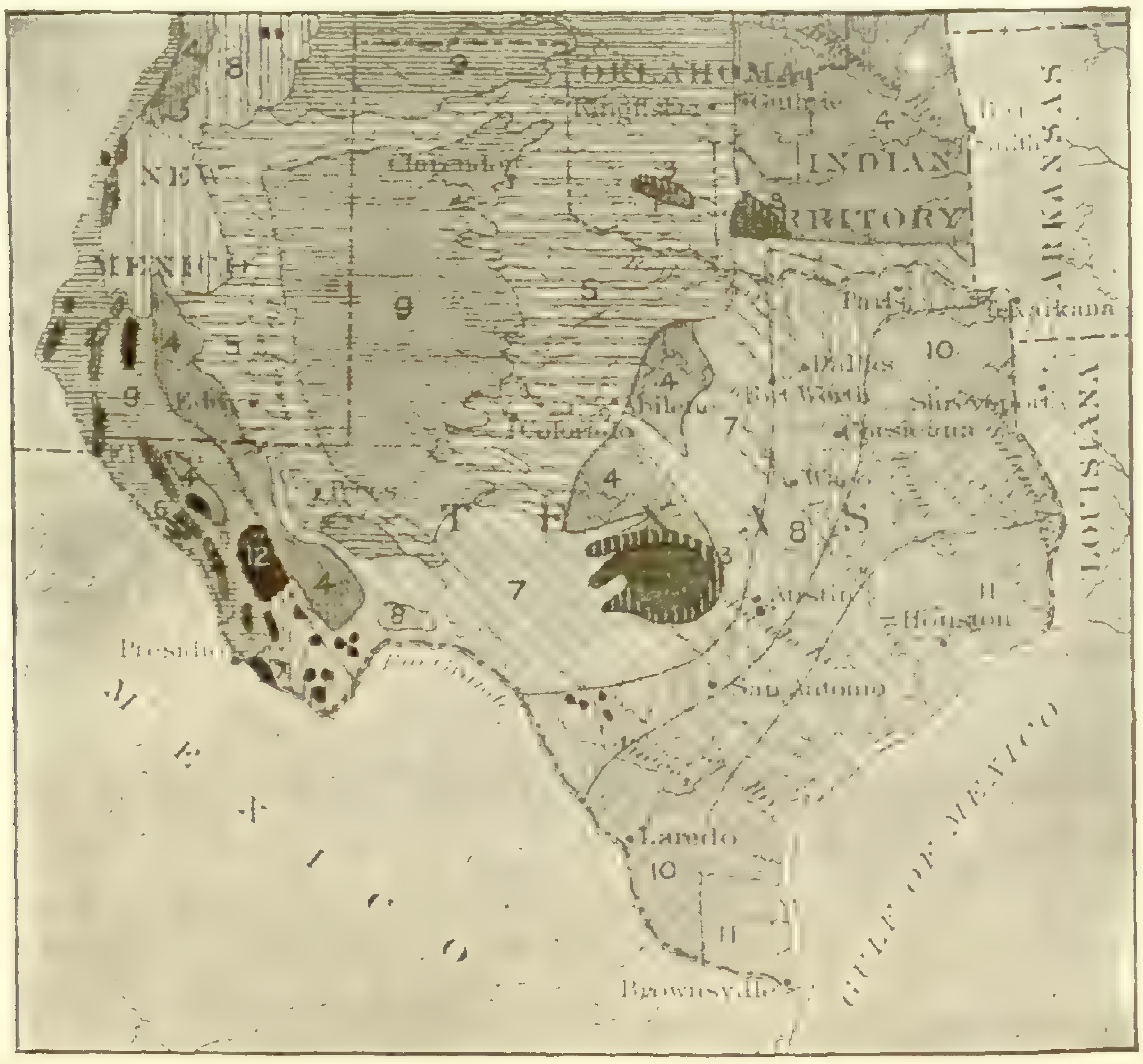
OKLAHOMA
Kingfisher
Guthrie
INDIAN TERRITORY
ARKANSAS
NEW MEXICO
Texarkana
Paris
Dallas
Fort Worth
Corsicana
Waco
Austin
Houston
San Antonio
Laredo
Brownsville
Presidio
MEXICO
GULF OF MEXICO
LOUISIANA
TEXAS
1
2
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FIG. 2.—Geology of the greater Texas region; *1*, Older Granites; *2*, Palaeozoic and Mesozoic; *3*, Cambrian and Silurian; *4*, Carboniferous; *5*, Permian; *6*, Jurassic; *7*, Lower Cretaceous; *8*, Upper Cretaceous; *9*, Non-marine Tertiary; *10*, Marine Eocene; *11*, Coast Neocene; *12*, Later igneous.—From Hill's Phys. Geog. Texas.

exhibited in their general aspect, is the most convincing demonstration of the identity of this region with the northern prairies, and its small affinity with the southern ones. The cultural possibilities still further emphasize the extremes of these two divisions of the Lower Sonoran zone. As regards moisture conditions, both are transitional between Austro-riparian and Lower Sonoran, but the Rio Grande plain is in the zone of rice, cotton, sugar cane, of fruits like the fig and pomegranate; while the northern prairie province is in the belt of corn, wheat, and oats, and of such fruits as the apple. In short, the two provinces are transitional both as to temperature and moisture zones, the Rio Grande to the semi-arid and arid tropical, the central prairies to the Upper Sonoran and Carolinian zones.

The extreme in the direction of Lower Sonoran arid conditions is reached in the bolson desert provinces of trans-Pecos Texas. Certainly westward of the prairie plains of the Stockton plateau one is within the arid plateau province of that part of the Lower Sonoran zone, which then prevails westward to the Pacific. Indices of this arid province are the Yucceae, Agaveae, Cactaceae, and genera like Fouquiera, Larrea, and Flourensia. Elements of this extremely arid portion overlap to some extent portions of the Edwards plateau and of the south debris slope of the Staked plains, as will be seen subsequently. Finally, the entire area covered by the Lower Sonoran provinces is occupied by the single and generally dominant *Prosopis juliflora* (mesquite), which, though dependent upon certain peculiarities of soil structure, is absent from no considerable portion of the zone, and in its growth and occurrence reflects the measure of climatic conditions prevailing in the several provinces. This species marks well the transition from Lower to Upper Sonoran on the Staked plains.

UPPER SONORAN.—This zone occupies the Staked plains and Panhandle above 3500 feet, the higher slopes and summits of the Guadalupe (except the highest points in the range), Davis, and other northern mountains above 4000 or 4500 feet, and of the Chisos mountains in the Great Bend above 6000 or 7000 feet. The summit of the Staked plains above 4000 feet has, as regards temperature, the climate of the southern half of Kansas, Illinois, and Missouri; but on account of low average rainfall and prevailing high southwest winds it has the characteristics of the high plains climate of western Kansas and Nebraska. In trans-Pecos Texas the Upper Sonoran zone is a series of islands represented by the isolated mountain summits rising out of the Lower Sonoran zone.

TRANSITION ZONE.—The highest peaks of the Guadalupe and Davis mountains possess a considerable number of transition herbaceous and shrubby species ranging north in the mountains of Montana and Washington, beside forest tracts of *Pinus ponderosa*, *P. flexilis*, and *Pseudotsuga taxifolia*, which are typical transition forests.

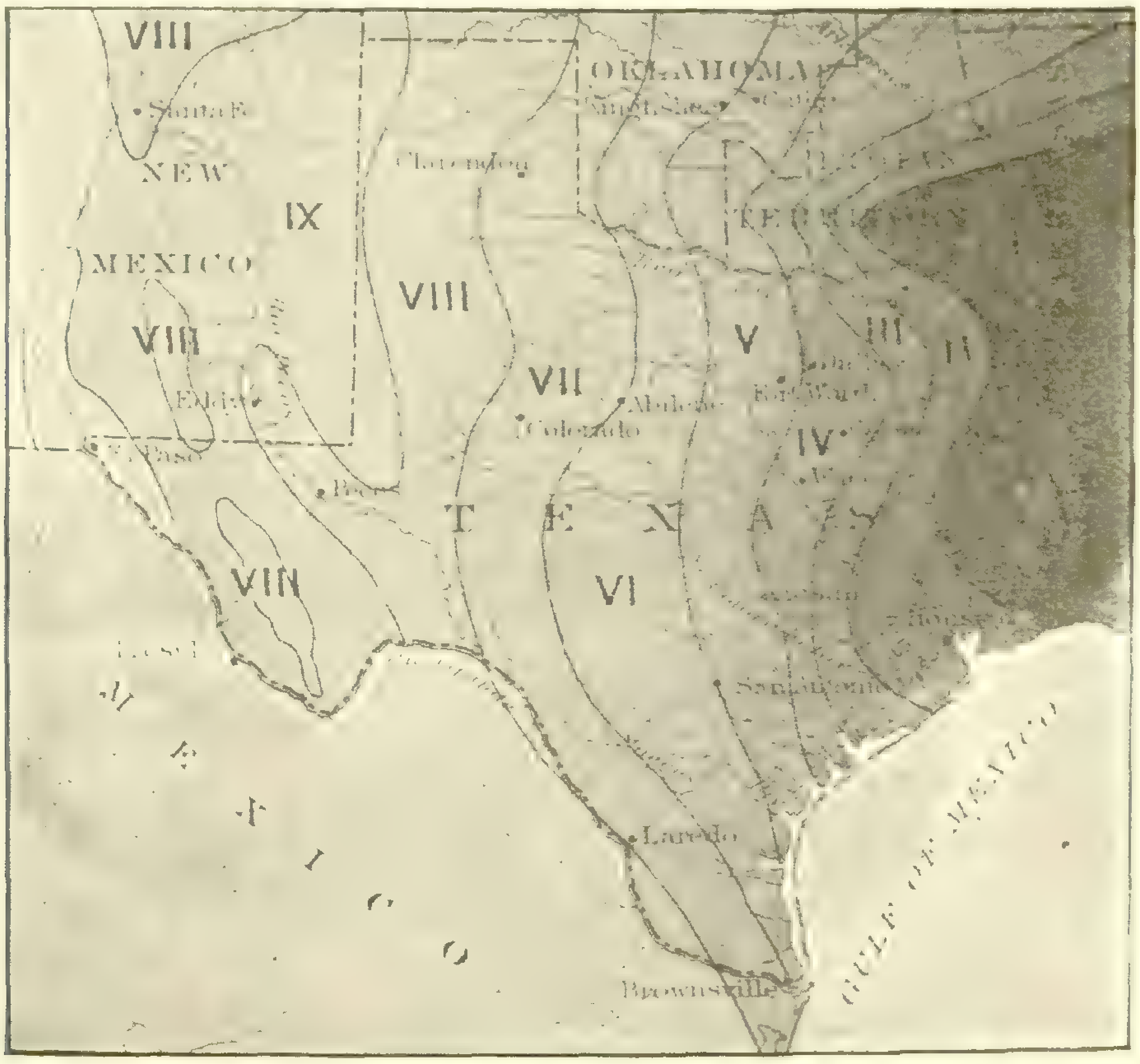
FLUCTUATIONS IN ZONAL BOUNDARIES.—If we accept the law of temperature control "that the distribution of boreal species southward is limited by the mean temperature of a few weeks during the hottest part of the summer," those annuals which begin their activity at a relatively low temperature, and complete their vegetative and fruiting period before the approach of summer temperature, would enjoy a distribution far within the Austral regions. To state the case differently, within the Lower Sonoran or semi tropical zone the lower temperature prevailing during February, March, and April, in which certain boreal species complete their period of fruition, would be for such species as truly a boreal zone as if they completed their fruition period during April, May, and June in correspondingly higher latitudes. This fact can account for the presence of such species as *Evax prolifera*, *Draba cuneifolia*, *Anemone Caroliniana*, *Corydalis aurea*, *Linaria Canadensis*, and others, within the borders of the semi-tropical zone. These all come into flower in the last half of February. This also explains how many prairie annuals, which are so abundant in their season as to give the dominant tone to the vegetation, may appear in this way successively over the whole Great plains area and south to Brownsville, or more frequently over the central prairies of Kansas, Missouri, and

Indian Territory to the southern extremity of the Rio Grande plain.

MOISTURE, WIND, AND LIGHT.

MOISTURE.

RAINFALL.— Beginning with an average fall of about thirty inches at the 98th meridian, the annual rainfall of the west Texas region decreases to nine inches at El Paso. This decrease is in general so uniform that the state may be divided into north and south zones of precipitation of five inches difference in the annual amount. The organization of vegetation with respect to moisture emphasizes these zones. The greatest interruption in their north-south equality occurs in the Guadalupe and Davis mountains, where the rainfall on the summits is fully double that of the bolson plains between the ranges (*fig. 3*).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Santa Fe
NEW
MEXICO
IX
VIII
OKLAHOMA
INDIAN
TERRITORY
Clarendon
VII
V
III
II
IV
VIII
El Paso
Colorado
Abilene
Fort Worth
Waco
T E X A S
VIII
VI
Austin
Houston
San Antonio
Laredo
Brownsville
GULF OF MEXICO
M E X I C O

FIG. 3.— Precipitation in the Texas region: *I*, over 50 in.; *II*, over 45 in.; *III*, over 40 in.; *IV*, over 35 in.; *V*, over 30 in.; *VI*, over 25 in.; *VII*, over 20 in.; *VIII*, over 15 in.; *IX*, over 10 in.— From Hill's Phys. Geog. Texas.

Of equal importance with the total quantity of rainfall for plant life is its seasonal distribution. Even in the eastern part of the area this is irregular and spasmodic, although a sufficient quantity falls on the average to maintain a fairly large percentage of mesophytic species of the Mississippi valley and Gulf regions (Carolinian and Austroriparian zones), and to insure reasonable certainty of yield from cotton, corn, wheat, and oat crops. But the vegetation west of the 98th meridian bears the marked individuality of the Lower Sonoran zone in its physiological adjustment to arid conditions.

Texas lies in a peculiar position with regard to atmospheric movements, which may account for the periodic and excessive variations in seasonal and annual rainfall. The El Paso region is clearly within the Pacific-Lower Californian field of climatic influence, while the Rio Grande plains province is mostly in the Mexican climatic zone. The Great plains type of rainfall predominates over the Staked plains, and generally far into the center of the state. The Gulf type scarcely extends west of the Balcones escarpment and Grand prairie, but occasionally it carries a season of high rainfall well toward the central provinces, as during the season of 1900 (*fig. 4*).

The mean annual rainfall at Austin is 38.88 inches. Its lowest record is 18.33 inches in 1879, and its former highest record, 51.79 inches in 1888, was exceeded during 1900. The rainfall from January 1 to November 1, 1900, reached 51.19 inches. This is a fluctuation equal to the total mean. The fluctuation between Gulf and Mexican type is shown in a remarkable degree at Brownsville, where the mean is 31.52 inches, the minimum 8.88 inches in 1870, and the maximum 60.06 inches in 1886, a variation of 167 per cent. of the mean. The amount of rainfall in a single month and its departure from the monthly average may be excessive. In the last case cited (Brownsville), the rainfall for September 1886 was 30.57 inches, or 23.27 inches above the September mean. The June rainfall at Fort Clark in 1899 was 22.32 inches, or 19 inches above the mean, over 75 per cent. of this excess falling in twenty-four hours. It thus appears that not only are the fluctuations extreme, but that a large percentage of the season's rainfall may be precipitated in two or three heavy thunderstorms. The effect of the consequent erosion is of significance for vegetation under certain soil conditions, as for example in the Red beds province, and in other places where too heavy pasturing has bared the ground of the soil-building grasses, as in the upper Rio Grande province. From these irregularities it follows that the vegetation has adapted itself to continuous drouths, and to sudden transitions from growing to dormant periods and back again.

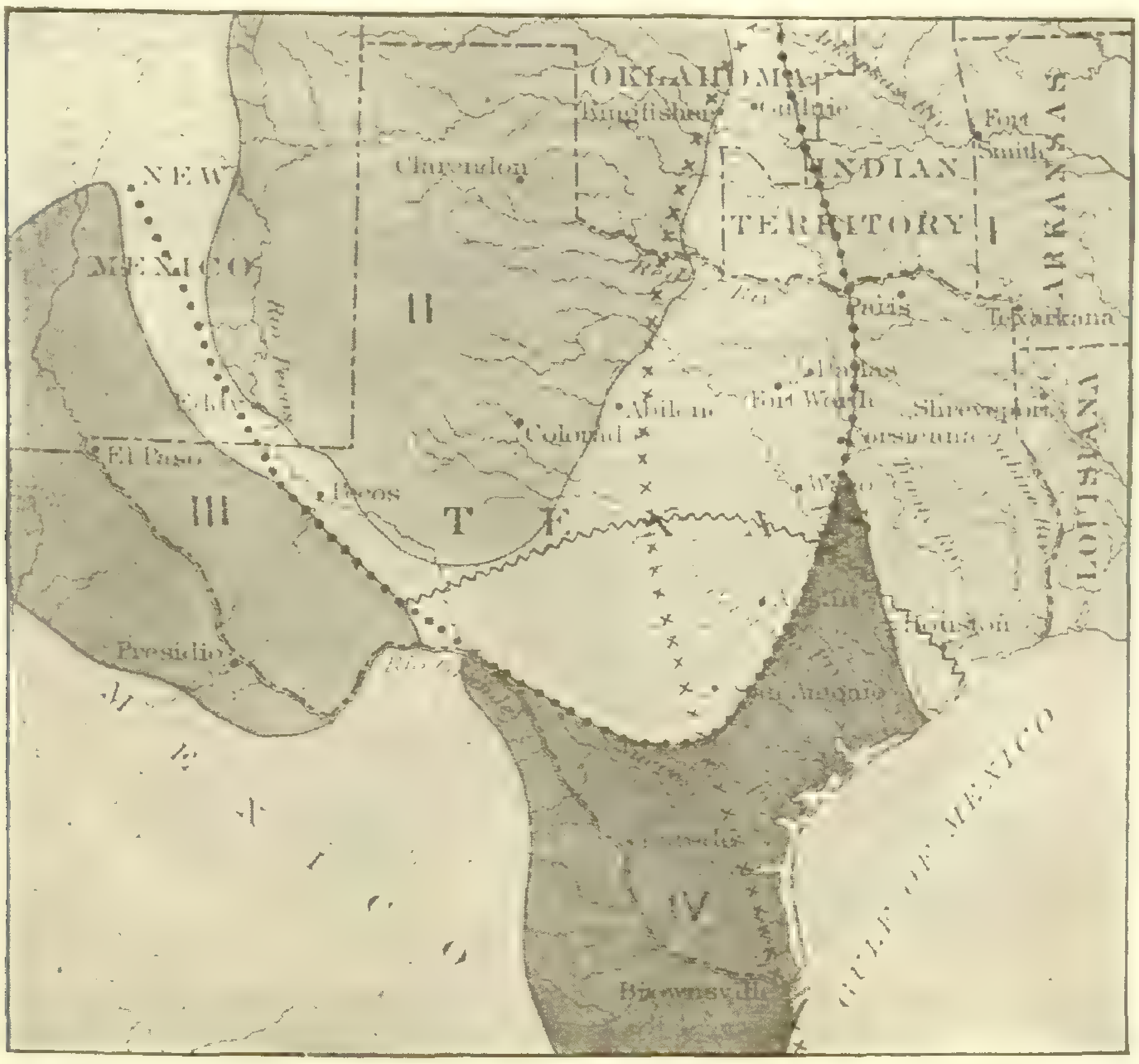
OKLAHOMA
Kingfisher
Guthrie
Fort Smith
ARKANSAS
INDIAN TERRITORY
I
NEW MEXICO
Clarendon
II
Rio Pecos
Red
Paris
Texarkana
Dallas
Fort Worth
Abilene
Colorado
Shreveport
Corsicana
LOUISIANA
Eddy
El Paso
Pecos
III
T
E
X
Waco
Austin
Houston
Presidio
San Antonio
Rio Grande
M
E
X
I
C
O
IV
Brownsville
GULF OF MEXICO

FIG. 4.—Types of rainfall in the Texas region: *I*, Gulf; *II*, Great Plains; *III*, Yuma; *IV*, Mexican; ×××, western margin of Gulf; ..... southern margin of great plains; 〰, northern margin of Mexican.—From Hill's Phys. Geog. Texas.

SOIL MOISTURE.—The relation of rainfall to vegetation after its precipitation is of importance, and is largely a result of geological structure and relief. A single illustration will suffice. In traversing the Rio Grande plain from Uvalde to Eagle pass in April of the dry spring of 1898, all the country covered by compact clay silt wash from the Balcones escarpment, being soil from which rainfall quickly flows away, was practically bare of grass and herbaceous vegetation. Even the streamway timber vegetation was shedding its leaves. On the outcrop ridges of Eocene sand, where all precipitated moisture had been retained and kept available, the landscape was fresh with grasses, composites, legumes, and many other annuals. This was repeated in a more noticeable degree during the same month in passing from Eagle pass to Carrizo springs, where again the compact clay and silt alternated with wide stretches of Eocene sand. The availability of underground water in the sand beds is evidenced by innumerable wind pumps, while in the clay silt country the surface water is collected in ponds.

HUMIDITY AND EVAPORATION CAPACITY.—The conditions of air moisture in the west Texas region have an important bearing upon the vegetation. As may be noted in *fig. 5*, illustrating evaporation capacity, this increases in proportion to the decrease in rainfall, reaching its maximum of 80 inches at El Paso, with this important exception, that in the high mountains of the Guadalupe and Davis ranges, where the rainfall is double that at El Paso, the evaporation capacity is 90 inches annually. This moistureless condition of the air under these circumstances reacts in several ways to pile up extremes of aridity. First, there is no blanket of vapor or clouds, so that the force of the sunlight is intense: and second, temperatures become extremely high during the day, and because of rapid radiation sink to a low point at night, except in the region of the Gulf winds. Under such circumstances the adaptations in the structures of plants are most strongly marked. It follows that moisture determines, far more than any or all other factors, the structural aspects of the flora.

Moisture determines, as we have already seen, degrees of intensity of the Lower Sonoran flora. Lack of moisture has diluted the tropical elements, the Gulf zone semitropical, the Austroriparian and Carolinian floras in the east, and the mountain transition flora in the west, all of which gradually disappear in the prevalence of intensely xerophytic species. On the other hand, increasing aridity has intensified the Mexican semitropical, the south plateau Sonoran flora, and the Great plains flora. The transition from the eastern mesophytic to the western xerophytic zones presents interesting phenomena of geographic range. For example, *Juglans nigra* is succeeded by *J. rupestris*, and *Juniperus Virginiana* by *J. sabinoides* and other species. Prominent Austroriparian and semitropical species, like *Pinus palustris*, *Magnolia grandiflora*, and *Persea Borbonia*, abruptly stop; and xerophytic Lower Sonoran and semitropical species as abruptly begin, as *Prosopis juliflora*, *Acacia Farnesiana*, and *Parkinsonia aculeata*.

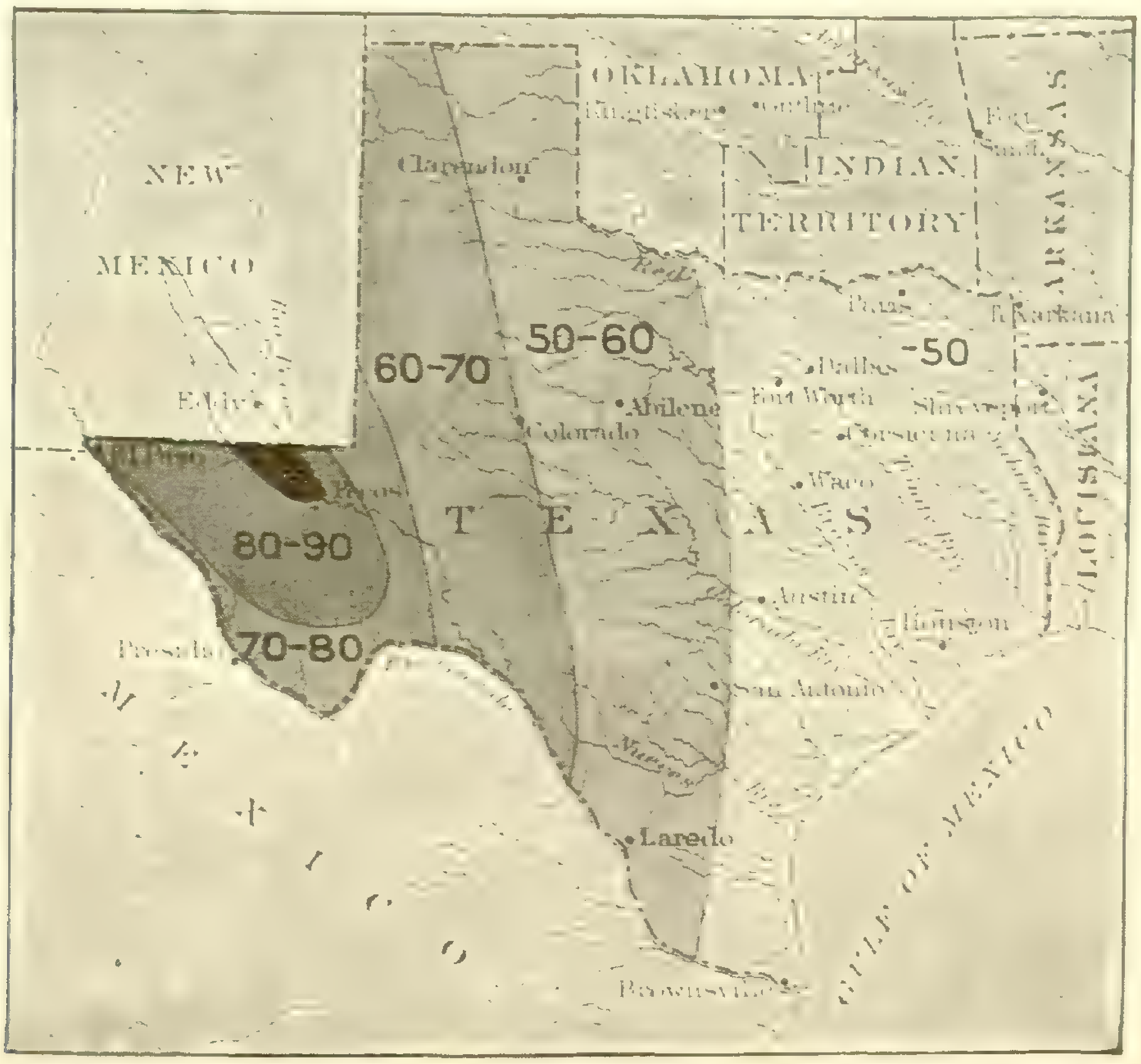
OKLAHOMA
INDIAN TERRITORY
ARKANSAS
NEW MEXICO
LOUISIANA
TEXAS
GULF OF MEXICO
Clarendon
50-60
60-70
-50
80-90
70-80
Abilene
Colorado
Fort Worth
Dallas
Paris
Waco
Austin
Houston
San Antonio
Laredo
Brownsville
Shreveport
Corsicana
Texarkana
Eddy
El Paso
Presidio
Red
Nueces
Pecos

FIG. 5. — Evaporation in the Texas region, in inches per year. — From Hill's Phys. Geog. Texas.

WIND.

The enormous expanse of the plains area in Texas and the daily heating of a thinly covered soil promote movements of air of very effective velocity, especially during the most active growing season. The average velocity per hour for the Gulf coast at Port Lavaca (observations taken formerly at Indianola) from January to July is fourteen miles, at Fort Elliott in the Panhandle 13.4 miles, at Abilene in the central plains province 11.9 miles. The prevailing direction in these cases, and for all the area east of the Staked plains and the Pecos river, is from the southeast, except for Fort Elliott, where the winds during January, February, and March are from the northwest (of little significance as they precede the season of growth). On the summit of the plains the velocity is even higher, and the prevailing direction during the growth period is from the southwest and west. The winds of trans-Pecos Texas are also prevailingly southwest, so that for the Staked plains and trans-Pecos Texas the winds are relieved of their moisture by long passage over arid plateau country. East of the Staked plains and of the Pecos the prevailing wind is from the Gulf.

The significance of these winds for plant life is as follows: (1) in their mechanical impact upon plants; (2) in rapidly carrying away moisture; (3) in erosion and transportation of soils; (4) in moisture-bearing capacity. As to the first point, the result is to dwarf and minimize arborescent growth, and to exclude plants with broad foliage, or herbaceous plants of tall growth. Trees on the coast prairie always incline strongly to the northwest, as does also the prairie mesquite in the Abilene country. On the summit of the plains, even with irrigation, groves of trees are very difficult to start because of the whipping, and bruising, and breaking of young branches and foliage by the wind. On the coast prairie windbreaks are essential in cultivating orchards. At Alvin the orchards where unprotected by windbreaks dwindle away toward the southeast exposure.

As the final effect of high wind is to promote rapid transpiration, this danger results in plants with sparse foliage of small sized leaves. This is brought about also by prevalent or frequent extremes of aridity due to intense heat and lack of precipitation throughout the region of high wind velocity.

In the third place, the transporting power of the wind has a marked influence on the selection of species. First, by dune formation and the assemblage of characteristic dune species, but particularly of sand-binding plants. This is true on the Gulf and on sandy stretches in the interior (Staked plains sand area, Rio Grande sand areas). In the second place, by the erosion and blowing away of soil-forming débris which tends to accumulate upon and modify arid patches, thus rendering the substratum almost naked rock or chalk or gravel, and inducing a new vegetation. The process of wind denudation is much more common, since after over-pasturing and dry weather thousands of acres are left unprotected by soil-binding grasses, and the soil being often a loose, fine silt, or adobe of sandy nature, is easily lifted by even a moderate breeze. It was shown above that such soils are also greatly washed by the heavy rainstorms which come at irregular periods.

As to the moisture-carrying capacity of the winds, of course the Gulf wind starts inland fairly well saturated, but meeting constantly warmer and drier conditions its relative humidity is greatly decreased, so that a precipitation of the moisture of a direct Gulf wind is not common.

LIGHT.

It would be of value if there were definite quantitative data as to the effect of light upon the vegetation of western Texas. Undoubtedly its effect is felt in the general dwarfing of the vegetation, and is plainly seen in the peculiar types of arboreal vegetation, as the "orchard tree" outline of crown. This is observed characteristically in the mesquite, but the live oak, water elm, post oak, and hackberry also assume this form. The mountain cedar is a compact low tree of oval or spherical outline, with diffuse branching from the ground. Undoubtedly the dull grayish-green of the vegetation is largely due to the effect of light, as there are probably fewer chloroplasts in any given assimilative cell. Also there are cases where the epidermis is so constituted as to diffuse light rays by reflecting facets, as appears to be the case in many cactuses and agaves.

A series of experiments was conducted by Professor H. Ness[4] to determine certain differences between the growths from seed of the same varieties of corn grown at Ithaca, New York, and at College station, Texas. Among other things, he showed conclusively that in Texas all varieties have a much shorter stalk than in New York, which he concluded was due to differences in the relative intensity of light, thus verifying previous observations.

In the trans-Pecos country the percentage of sunshiny days is nearly as great as in the maximum region of central and southern California. Where the Gulf winds prevail, there is a relatively high percentage of cloudiness and humidity, which reduces the total light effect. But the percentage of sunshiny days does not express the real effect of light upon vegetation in this region; it is the actual intensity or quantity present at any given hour of sunshine. The sun's rays are almost at the maximum intensity during the vegetative season, and their intensity is undiminished by atmospheric moisture over most of the area. Furthermore, the rock, gravel, chalk, or clay, lacking a green covering of vegetation to receive and subdue the light, reflect it in blinding intensity. Partly on this account, and partly because of lack of air, moisture, and rainfall, there is no densely shading vegetation characteristic of the region except in well-watered cañons. The dominant mesquite, huisache, retama, and numerous other Mimoseae, with their feathery foliage only loosely filter the light, but do not interrupt it. The junipers and pines of the hills and mountain slopes of the Lower Sonoran zone are also relatively shadeless trees, and the scrub oak and the chaparral species generally cast only a thin shade. As a consequence, the shade loving plants west of the 98th meridian are confined to moist crevices or watered cañons and sheltered water courses. This feature is emphasized by the absence of shade loving pteridophytes, and the general occurrence on the exposed rock of eroded areas of sun loving ferns and club mosses.

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[4] Transactions Tex. Acad. Sci. 2: [part 1]. 1898.

PHYSIOGRAPHY AND GEOLOGY.

In general the "greater Texas region" of Hill, to borrow his illustration, lies as a stairway leading from the coast by a succession of steps to the cordilleras. On the west there is a balustrade formed by the southern prolongation of the Rocky mountain cordilleras and plateau; on the north the balustrade is the Ouachita system, extending east and west in Oklahoma and the Indian Territory. The slope leads up from the Gulf level to 5000 feet at the base of the cordilleras at the northwest. The geological areas are the "stair steps," speaking approximately. Beginning with the latest, they are the coastal plain (coast Neocene), the Fayette prairies (marine Eocene), the Black prairie (Upper Cretaceous), the Grand prairie (Lower Cretaceous), the denuded areas of the Granite country, the Carboniferous sandstones and shales, the Red beds (Permian), and finally the Llano Estacado (non-marine Tertiary). The "balustrade" of the trans-Pecos mountains and plateaus (except the Stockton plateau, which is part of the Great plains area) is quite distinct from the regions just cited. The tilting of the strata and weathering and erosion have given rise to diverse physiographic features, which are in close harmony with the geologic structures and strongly reflected in the vegetation (*figs. 1, 2*). Since the edaphic factors stand out so prominently in determining plant formations, they will be given a proportionate prominence in this discussion. In general, the physiographic and geologic provinces as defined in Hill's *Physical geography of the Texas region*[5] are employed in this paper, except that the Great plains region is made to include all east of the front ranges of the trans-Pecos Texas and north of the Rio Grande plain, with meridian 97.5° as an arbitrary boundary on the east. This is done because the physiographic ecology of the vegetation is most significant when it is borne in mind that the present conditions are but a stage in the leveling down of a former higher plain which covered this entire area, and whose remnants we have in the Great plains proper, the Edwards plateau, and buttes

[5] Topographic atlas of the U. S. Texas folio.

and mesas scattered all over the central prairie provinces. The process of leveling is in various stages in different places, such as deep dissections in the southern half of the Edwards plateau, undulating prairie in the Grand prairie province, a flat plain in the granite area with rugose surface caused by projecting granite

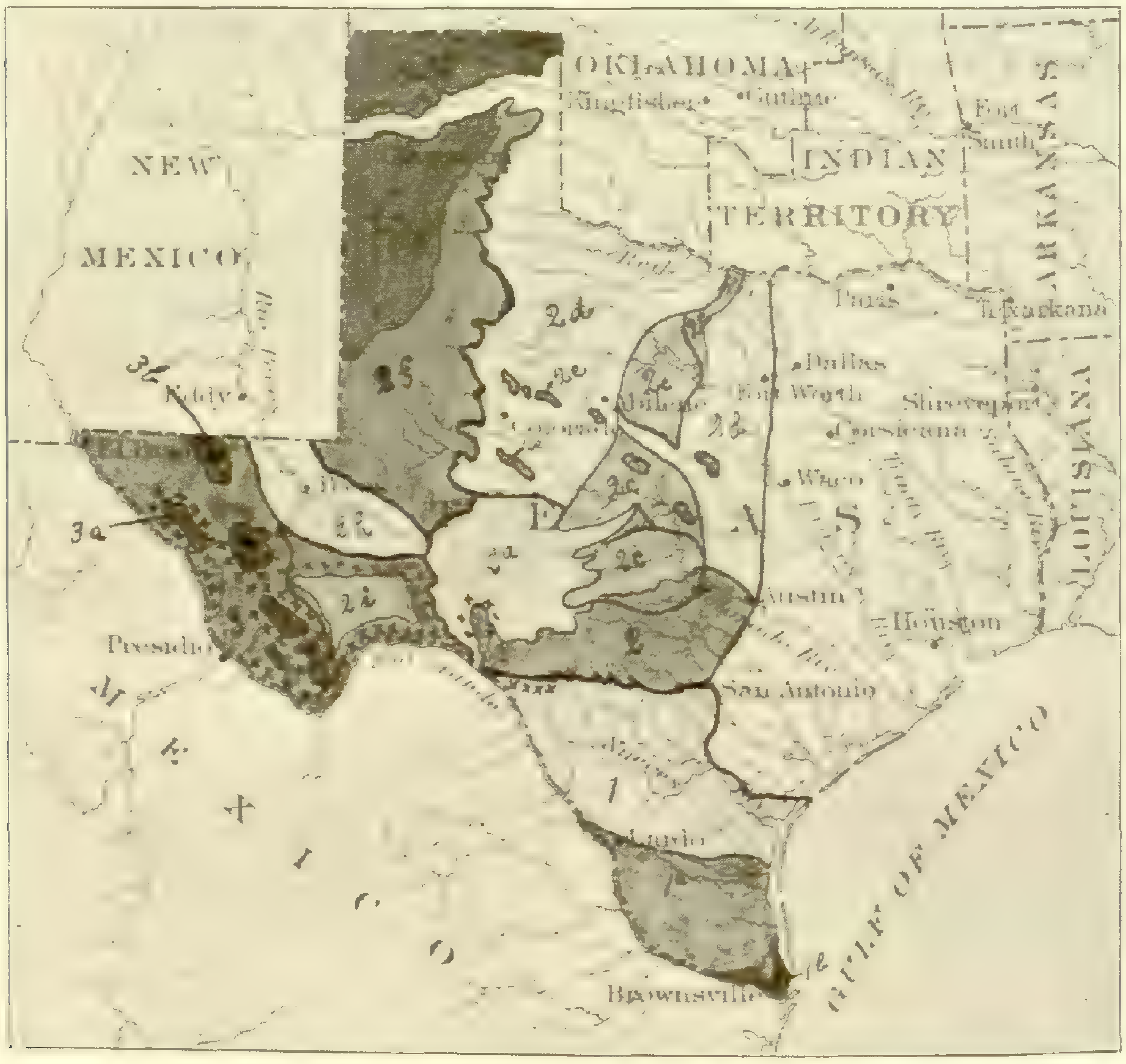
OKLAHOMA
Kingfisher
Guthrie
INDIAN TERRITORY
Fort Smith
ARKANSAS
NEW MEXICO
Eddy
3b
2d
2e
2f
Paris
Texarkana
Dallas
Fort Worth
Shreveport
Corsicana
LOUISIANA
Abilene
Colorado
2b
2c
Waco
E
A
S
3a
2h
2i
2a
Austin
Houston
Presidio
2
San Antonio
M
E
X
I
C
O
1
Laredo
1a
1b
Brownsville
GULF OF MEXICO

FIG. 6.—Vegetation provinces of the west Texas region, chiefly on the basis of physiography and geology: *1* to *1b*, Rio Grande plain, chaparral region (*1*, Lower Sonoran transition to Austro-riprarian and semi-tropical; *1a*, semi-tropical, *1b*, dilute xerophytic tropical); *2* to *2i*, Great Plains region (*2*, Edwards plateau xerophytic timber province; *2a* Edwards plateau plains, grass formations; *2b* Grand prairie transition, between Lower Sonoran and Austro-riparian, grass formations, adobe vegetation, butte and escarpment timber; *2c*, post oak formation on granite, Carboniferous, and upper cross timber sands and gravel; *2d*, grass prairie formations of Red beds province, Lower Sonoran with elements of Upper Sonoran; *2e*, erosion remnants (buttes) of Staked plains and Cretaceous area, xerophytic timber; *2f*, Staked plains Lower Sonoran; *2g*, Staked plains Upper Sonoran; *2h*, Toyah basin, Pecos valley province; *2i*, Stockton plateau province, grass formation and Yucca belts); *3* to *3b*, provinces of Rocky mountains and south plateau slope (*3*, extreme Lower Sonoran, bolson flora, chaparral, Yucca-Agave-Cactus formations; *3a*, Upper Sonoran; *3b*, Rocky mountain transition).

masses. These various phases in the process of wearing away the former plain and leveling up the denuded areas constitute the edaphic conditions which determine the general types of vegetation formation prevailing in the several provinces. These might serve almost equally well as designations of vegetation provinces. The provinces here referred to are the following: the Rio Grande plain; the Great plains region, embracing the Edwards plateau, the Grand prairie, the granite area, the Carboniferous area, the Red beds prairies, the Staked plains, Toyah basin, and the Stockton plateau; the south plateau of the Rocky mountains, embracing isolated mountain masses and cañons, grass plains, and bolson deserts.

PLANT FORMATIONS.

The classification of plant formations employed in the following pages is based chiefly upon local conditions of soil, geologic structure, and physiographic features, that is the formations are edaphic. For example, rock formations, forest formations, and salt basin formations exist because of local soil structure or content. In the case of grass formations, climatic factors, especially moisture, play an important part, not only in determining the existence of a grass formation as opposed to a forest formation, but also in determining the special association of species in the different formations. For example, although the physical structure of the Staked plains is most favorable to forests, such formations are naturally excluded by scantiness of rainfall; and in the Rio Grande plain the pigmy forest of chaparral succeeds the dense mesophytic forests of the Atlantic coast plain because the factor of moisture has suffered so great reduction. In every case the particular type of formation existing upon a given local area depends upon the local conditions of physiography and geology. For example, of the forest formations the post oak type is always present upon sand and gravel beds. The streamway cañon, hill bluff, and escarpment forests are all products of the soil conditions prevailing where they occur; for, although their differences are due to differences of moisture, these are a result of the physiographic and geologic peculiarities, and may occur independently of rainfall and humidity.

The plant life of the region in general may be included in the following formations: (1) grass formations, (2) woody formations, (3) succulent formations, (4) rock formations, (5) halophytic formations.

I. GRASS FORMATIONS.

The consideration of plant formations in western Texas may begin appropriately with the grass formations, for, excepting only the highest mountain summits of trans-Pecos Texas, the climate is a "grass plains climate," and the grasses may be said to form the matrix of the vegetation of the region. Texas is thought of commonly as a land of grasses, and properly so as regards the portion considered in this paper. Under what may be called natural conditions, to distinguish them from conditions which prevail under the present era of exploitation, the grass formations held their own in the perpetual struggle against woody vegetation. With the advent of the cattle business, however, this advantage was lost, and the present is an era of the rapid encroachment of timber formations. These phenomena and their causes will be specially considered in a subsequent paragraph. Mention is made of the matter here to explain that in discussing the grass formations as they now exist we are dealing with a vegetation which, though still the dominant type, has not only a more restricted distribution than formerly, but is undergoing perceptible changes, not only in restriction of its area as the dominant formation, but in the association of species within the formation.

Along with the grass plains vegetation will be discussed those types of formation which, though distinct enough as formations periodically, never for more than a brief period form the dominant vegetation, and are in every case distinctly a prairie feature. Such are the prairie annuals (generally mesophytes) and the lignescent perennials (tropophytes).

In the present discussion the formations are taken up by geologic and physiographic provinces, because they seem not to be distinguished so much upon floristic as upon ecologic grounds. Temperature conditions will be seen to paly a rôle as between a province in the extreme south and one in the extreme north, but even then chiefly in the floristic content of the annuals and lignescent perennials of the prairie formations. Again, the breadth of area from east to west, following the lines of decrease in rainfall, gives the grass formations of the eastern provinces a physiognomy differing from that of the extreme western. Finally, as previously mentioned, since edaphic factors exert such a marked control upon formations, the consideration of the grass formations by provinces will give the full force of these factors.

A preliminary word may be said in reference to the grass formation of the region as a whole. It was stated above that the climate of the region is a grass plains climate, and that the grasses form the matrix of the vegetation, this being true even where they are not the dominant element. Taking the region as a whole, there is a wide range of climatic (hydrometeoric) conditions between the east and west boundaries. But even in the province of greatest rainfall, climatic conditions, together with geologic and physiographic conditions, result in a decidedly xerophytic vegetation. The grass vegetation is the chief exponent of the xerophytic conditions, and certain ecologic types of grasses are found through the entire region, as *Bulbilis dactyloides*, the specifically designated "buffalo grass." Throughout the entire region, also, the dryness of air and brilliancy of sunshine cause adaptations to rapid transitions from active growth to dormant conditions, great quantities of nutritive materials being stored in the dormant parts.

THE RIO GRANDE PLAIN.

PHYSIOGRAPHY AND GEOLOGY.—The area here included in the Rio Grande plain is really the continuation of the Atlantic coast plain west of the 98th meridian. It is in general a triangle, whose vertices lie at San Antonio, Del Rio, and Brownsville. At the north, along the base of the triangle from San Antonio to Del Rio, the plain ends abruptly at the southern margin of the Great plains region, which is here marked by a sudden downfall, the Balcones fault escarpment, which here has an altitude of about 1000 feet. From the foot of this escarpment the plain slopes gradually to Gulf level. The Rio Grande plain of geologists, called also the Rio Grande embayment, is described as a constructional plain lying between this escarpment of the plains and the east front of the Mexican cordilleras. Its surface consists of the sheet flood débris of these two border regions, and its individuality, as distinct from the Atlantic coast plain eastward, lies in its construction and its surface weathering under far drier conditions than those which prevail eastward.

The sheet flood débris from the margin of the plains does not cover all of the Rio Grande plain as here defined. The flat coast prairie with its compact clay structure still extends along a narrow belt toward the lower Rio Grande. From Brownsville northward to the middle of the region extend vast sand plains, tongues of which reach well up toward the escarpment border. The flood débris lies in coarser or finer beds over the northern half of the plain, with exposures of arid clays, flat silt plains, or ridges of coarse gravel. Add to these features the basalt extrusions both along the northern margin and in the southern sand plains, and the streamway erosions through the various deposits, and we have the factors which not only combine to determine different types of grass formation, but have also figured prominently in favoring the encroachment of the woody vegeation, chiefly the chaparral formations.

CLIMATIC CONDITIONS.—The temperature conditions are of great significance to vegetation in this province, but only indirectly do they react upon the character of the grass formations. This indirect control consists chiefly in permitting the occurrence of woody species that require high annual temperature (Mimoseae for example), which, with certain artificial barriers removed, the burning of the grass notably, are capable of waging a successful struggle against grass vegetation. A further result of temperature conditions upon the grass formation is to determine, in conjunction with moisture, the floristic content of the subordinate elements in these formations — the mixture of annuals and lignescent perennials with the grasses.

With regard to moisture conditions in general, scant rainfall, low humidity, and brilliant sunlight, are such as to give the grass vegetation a pronounced xerophytic structure. In this respect the grass formations agree with those of the dry plains westward, in which, with the approach of the resting period, coincident commonly with rainless periods, the aerial parts become "cured;" that is, they die, retain without loss their nutritive qualities, and remain in a good state of preservation.

Since the 98th meridian is a mere arbitrary boundary, selected with reference to separating approximately the xerophytic vegetation regions from the mesophytic, it is evident that at the eastern border of the Rio Grande plain, especially in the coast region, the grass formations approach more nearly the mesophytic structure; while at the west, along the Rio Grande, they approach the pronounced xerophytic aspect of distinctly arid regions.

With respect to the relation of grass formations to woody formations in the Rio Grande plain, the encroachment of the latter has been so vigorous as practically to destroy continuous areas of open grass formation. Much of the province is covered by impenetrable thickets of chaparral. There are broad stretches of savanna where the grass formation is more open, but the areas are studded with isolated individuals or clumps of live oak, or by open post oak formation.

On the basis of geologic structure and soils, three types of grass formation may be distinguished: (1) those of the flood débris plains; (2) those of the sand plains; and (3) those of the coast prairie. The first two are by far the most extensive and important. The third is but a slight extension of the coast prairie formation which is so characteristic on the Gulf coast from central Louisiana westward to our region.

THE FLOOD DÉBRIS PLAIN.—The flood débris from the Cretaceous formations of the Edwards plateau covers approximately the upper half of the Rio Grande plain, the altitude being from 500 to 900 feet. The level stretches of this part of the plain are covered with finer silt débris, the mesquite-chaparral plains. There are arid clay hills in the Eagle pass region, and coarse gravel and stony slopes nearer the escarpment, besides basalt cones or ridges and the outlying block of rough hills (Anacacho mountains).

Floristically the grasses are chiefly of genera making up the buffalo grass range of the plains northward. On the rougher areas, especially westward, the extreme xerophytic conditions give the aspect of the arid plains. The associated species are chiefly lignescent perennials, or perennials with thick fleshy or tuberous roots, such as *Jatropha spathulata sessiliflora* on stony or gravelly soil, *J. macrorhiza* on loose silty soil, and numerous other Euphorbiaceae and Nyctaginaceae peculiar to warmer lower Sonoran areas.

The grass formation on these areas has been very much reduced by over-pasturage, so that during drouth periods vast tracts lie quite bare of grass vegetation. In this condition pastures not wholly beset with chaparral have the appearance of fields lying beaten and fallow. So great has been the depletion of grasses that during certain dry years it was stated that from fifteen to twenty-five acres of land were required to pasture a single cow. What permanent effects on the grass formation will result upon areas so denuded it is not yet possible to say, except that the chaparral will cover the entire plain. The grasses have great recuperative power, and it is said that after periods of abundant rainfall the earth is covered again with a close grass formation. No doubt a period of rest from excessive pasturage would enable them to recapture fully much lost ground. Of course, with the presence of the chaparral and the new relations it involves, the original grass formation of open sunny plains will suffer some material changes. This subject offers a field for special investigations.[6]

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[6] SMITH, JARED G.: Grazing problems of the southwest. Bulletin 16, Division of Agrostology, U. S. Department of Agriculture. 1899.

THE SAND PLAINS.—These sandy grass plains constitute the most considerable feature of the southern half of the Rio Grande plain, and arms from them reach well toward the northern boundary. In some areas the sands are so deep and shifting as to render any stable vegetation impossible. Such areas are not yet well enough known to discuss here. The conditions as regards earth moisture in the sand plains are such as to leave them covered with grass vegetation and accompanying herbaceous plants when the flood débris plains are bare of the corresponding formation. This is because they are not only better receiving areas, but the underground water is more available, for as the altitudes are low the distance to water is not great, and the open texture of the ground aids in that short distance in bringing water to the surface vegetation.

The grass formations of the sand plains are different from those of the flood débris plains in two important respects; first in the more open character of the formation, and second in their floristic content, in which the secondary elements—the prairie annuals and lignescent or succulent perennials—are especially involved. The open character of the grass formation permits an uncommonly varied growth of sand plains species. Many of the more important of these are of semitropical affinities, and hence not found in the more northerly or more elevated provinces.

THE COAST PRAIRIE.—This is typically a sod prairie with grasses and sedges of mesophytic requirements, and annuals similarly adapted to wet, low, coast lands. Such prairie is continuous between Houston and Corpus Christi, except for streamway interruptions; though in passing westward along the line of decreasing rainfall the formation gradually becomes of xerophytic stamp, and the semi-marsh land species are succeeded by grasses of the plains. Within the province of the Rio Grande this formation passes into that of the sand plains.

UNIVERSITY OF TEXAS.

[*To be continued.*]

[illegible]

A STUDY OF THE SPORANGIA AND GAMETOPHYTES OF SELAGINELLA APUS AND SELAGINELLA RUPESTRIS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY XXXI.

FLORENCE MAY LYON.

(WITH PLATES V–IX)

SELAGINELLA APUS.

SPORANGIUM.—It is by no means an easy matter to determine the origin of the sporangium in *S. apus.* It is quite possible, from a number of slides, to select a series which shall seem to prove that the archesporium consists of two superficial cells originating just above the axil of a sporophyll (*figs. 3, 4*). It is equally easy to procure evidence that a single epidermal cell initiates the sporangium (*figs. 1, 2, 5*). This single cell may be either upon the sporophyll or removed by several intervening cells from its base. The exact line of demarcation between sporophyll and axis is indeterminate. The difficulty lies in the fact that until the sporangium is well established, consisting of some half dozen or more cells, there are almost no indications in the structure, or size, or staining qualities of these cells to distinguish them from the vegetative tissue. Moreover, a sporophyll originates in close proximity to a sporangium (*fig. 5*), and at about the same time and until it has established an apical cell there is no way of distinguishing it from a young sporangium. These facts render cross and tangential sections well nigh useless for an interpretation of the earliest stages. From serial radial, *i. e.*, vertical, sections of the strobilus, if cut with due reference to the phyllotaxy, it is possible to form conclusions by comparison of the series of sporangia and sporophylls in the same rank and of different ages that appear in an exact median section. It is evident that the number of such sections which may be obtained by ordinary means is very limited. I found it necessary to imbed the strobili singly, examine each section as its plane approached the median region, and constantly alter the angle of the paraffin block in the microtome, until by the vascular strand of the axis and the leaf traces of the older sporophylls I could estimate approximately the section sought. Even with these precautions, I was not infrequently doubtful as to whether a cell that appeared in the right place theoretically for an archesporium might not be the initial cell of a sporophyll from the next rank that a slightly oblique section would display. These explanations are necessary, for after much painstaking study of many sections of tips of very young strobili, I find myself becoming less certain of there being a definite rule governing the initial phases of the sporangial growth. In many median longitudinal sections cut in the manner described above, a single epidermal cell projects from the surface in a vertical line between the youngest sporophyll and the apical cell of the strobilus. Occasionally it takes a deeper stain than the neighboring cells. There are usually from ten to twelve cells between it and the apical cell, and two or three between it and the subtending sporophyll (*fig. 5*). Quite as often this projecting papilla is composed of *two* cells of equal size lying in the vertical line (*figs. 3, 4*). In either case periclinal walls are formed, cutting off one or two cap cells (*figs. 2, 5, 6*). From the hypodermal cell or cells, thus formed, originates the sporogenous tissue. From the cap cell, which divides much more rapidly, the sporangium wall is formed. It is possible, I think, to determine in sporangia of various stages, nearly up to maturity, whether in a given case it originated from a single epidermal cell or from the two superimposed cells. In the second case, the complex of cells resulting from each of the two primary cells consists of more regular radial rows, and there is a quite definite plane of cleavage between the two groups. The only other interpretation of appearances like *figs. 6* and *8* is that the primary single archesporial cell divided first anticlinally, thus producing the superimposed cells, each of which then cuts off a cap cell. I have sought in vain, however, to establish that the first two are sister cells. When the sporangium consists of from four to six cells (*figs. 6, 7, 8*), the hypodermal cells assume a different appearance when stained, which distinction is maintained thenceforth in the development, and establish their identity as primary sporogenous cells. There is no apparent regularity in the order or plane of their division, with the exception above stated. The tapetal cells are differentiated very early in the history, and are the peripheral sporogenous cells which assume a more symmetrical shape and regular arrangement (*fig. 10*). A few of the cells in this layer, lying directly above the pedicel of the sporangium, appear to be derived from the vegetative cells in that region, and are not the lineal descendants of the archesporial cell.

Simultaneously with the differentiation of the tapetum the sporangium wall divides into two layers by anticlinal partitions (*fig. 10*). The outer layer soon surpasses the inner in the size of its cells (*fig. 11*). A pedicel develops by the multiplication of the sterile cells next to the axis and beneath the sporogenous mass. The megasporangium cannot be distinguished from the microsporangium until the moment when the cells of the sporogenous tissue cease to divide, separate from one another, and float in the sporangium. At this period, if one or two cells are more regular in form, stain more deeply, and possess a larger nucleolus, they are megaspore mother cells (*figs. 13, 35, 36*). The microspore mother cells are not distinguishable until the karyokinetic figures develop that precede their division into spores. A comparative count of the microspore mother cells in this stage and the cells in a corresponding megasporangium indicates that there is at least one more period of cell division in the former than in the latter. A cytological study may determine other means of identifying the two.

MEGASPORES.—The megaspore mother cell becomes nearly isodiametric, enlarges, stains deeply, and lies near the tapetum (*figs. 13, 35*). Apparently the mother cell never originates far within the sporogenous tissue but always near its periphery.

Infrequently two mother cells occur, and these may go through all the later stages of development, thus forming eight spores in a megasporangium. Normally the membrane of the single mother cell becomes distended by the imbibition of fluid that has been poured into the sporangial cavity from the tapetum. Two successive divisions follow each other with great rapidity. The spindle of the first division I have seen but a few times; the two that follow, I saw more frequently (*figs. 16, 17*). These are extremely small and delicate, occupy the middle of the cell, and are soon much obscured by fibers which arise in the surrounding protoplasm. These fibers at first radiate in all directions from no definite center, but later assume the form of a sextuple spindle with the four daughter nuclei at the poles. No cytological work was attempted, beyond determining the method by which the spores originate, but it is evident even from a cursory examination that there is some connection between the enveloping spindle fibers and the two lumps lying against the nucleus which are represented in *figs. 11, 13, 15*. In the meantime there has appeared a new membrane just within the mother cell wall (*fig. 15*). It is very delicate, but of unequal thickness, and can be detected only in particularly fortunate sections. Whether this membrane arises by cleavage from the mother cell wall, or *de novo* from the protoplasm of the cell, is necessarily a matter of speculation in an object so small. Nuclear plates form across the spindles, and the mother cell divides into four spores tetrahedrally arranged. At the moment of their separation the nuclei lie near the bases of the spores, which correspond in position to the poles of the sextuple spindle, but soon move toward the apices (*figs. 16–18, 22*). As the spores increase in volume, by their pressure outward, and by a folding inward on the part of the irregularly thickened special mother cell membrane above described, the tetrad presents the appearance of a four-lobed body surrounded by a single envelope whose continuity is not broken, floating in the fluid that fills the distended spore mother cell membrane (*figs. 17–19*). Either the special mother cell membrane itself thickens, or a new coat is formed upon its inner surface. This is the exospore (*figs. 20–22*). The spores increase in volume, but the exospore expands so much more rapidly than does the protoplasmic content, that the latter is left in the apical portion of the spore cavity as a tenuous spherical vesicle of protoplasm filled with a limpid fluid (*fig. 37*). A single very small nucleus, in which with difficulty may be seen one or two nucleoli, lies in the region nearest the spore apex. The rest of the spore cavity between the vesicle and the exospore is filled with a limpid fluid of the same nature as that which occupies the space between the tetrad and the mother cell membrane. Soon hair-like radiations appear traversing these fluid regions (*figs. 42, 43*), whose general direction is from the spore mother cell membrane toward the center of the tetrad. A thick layer which stains very deeply appears upon the inner face of the exospore (*fig. 37*). The latter maintains its more rapid rate of growth and soon afterward is widely separated from this layer, by a space filled with the liquid and the radial fibrillae (*figs. 38, 42*). The sculpturing of the exospore begins almost immediately upon its inception. The spines are laid down by depositions of matter derived from the liquid between the exospore and the mother cell membrane (*figs. 42–46*). -presumedly from material of [illegible]

As the megaspores increase in size, they are forced apart by the liquid in which they float seeping in between them (*figs. 38, 42, 43*) and the exospore is ruptured between the spores in such manner that each presents the appearance of a tetrahedron with a hemispherical base and three plane triangular faces. The tearing apart of the spores leaves a trefoil-shaped cleft extending from the apex along the three ridges between the triangular faces, and bounded by the flaring flaps of the torn exospore (*fig. 58*).

The sterile mother cells in part disappear by dissolving in the slimy fluid in the sporangium cavity, but not until the exospore is well developed. Some persist however throughout the development of the gametophyte and perhaps may grow slightly; they never divide.

FEMALE GAMETOPHYTE.—The spore is but a small fraction of its final volume when the sexual generation begins, thus overlapping the asexual (*fig. 44*). The initial steps of the female gametophyte development are the rapid expansion, without corresponding increase in thickness, of the protoplasmic vesicle, and the division of its nucleus. The nuclei divide by karyokinesis, and with each successive division become larger (*figs. 45, 46*). The thick envelope surrounding the vesicle stretches, becoming proportionately thin as its surface increases, until it comes to lie against the inner surface of the exospore. At this stage it consists of two distinct layers, the endospore and mesospore, both mere films which may be readily detected, as they stain differently and are easily torn apart (*fig. 46*). The gametophyte at this stage thus consists of (1) exospore, still growing, (2) mesospore; (3) endospore; (4) the protoplasmic vesicle, consisting of a very thin and homogeneous layer of protoplasm applied to the inner surface of the endospore, in whose apical region are imbedded numerous large, ovate, flattened nuclei; and (5) a large central vacuole filled with a watery fluid in which are suspended many oil drops.

Beyond the increase in the number of nuclei, which preserve about the same relative distance from one another, there is no further change until the spore membranes complete their growth. When the maximum size is reached, fibrillae arise in the protoplasmic vesicle at the apex, and radiate downward over its surface, blocking it off into irregular areas, each of which contains one or more nuclei (*figs. 49, 51, 52*). Simultaneously the protoplasm becomes invaded with masses of granular matter, and encroaches on the space occupied by the vacuole. Nuclear divisions take place radially, and so rapid is this process that frequently the spindle fibers of three and four generations of nuclei may be seen in a single section. The fibrillar radiations permeate the protoplasm, keeping pace with its increase in thickness. As the central vacuole diminishes in size, its contents change in appearance from an emulsion to a turbid fluid thickened with granules (*fig. 53*). The protoplasmic fibrillae apparently are concerned with the distribution of this nutriment before cell walls are formed. They have the appearance of streams bearing granules. The final and penultimate divisions of the nuclei are distinguished by the appearance of nuclear plates and spindles of quite different appearance, which result in the formation of definite cells with cell walls, each containing a single nucleus (*figs. 26–28*). At this stage, each nucleus is so surrounded by a mass of proteid as to be completely obscured. The only cells not thus gorged are a limited number which lie in the upper layer nearest the apex, beneath the trefoil-shaped cleft in the exospore (*fig. 54*). By continual multiplication they form a prothallial cushion, which widens the breach and bulges through. These cells are much smaller than those filled with the food supply. There may be from three to five layers in this cushion. There is no diaphragm between the region designated the prothallial cushion and the mass of storage cells underlying it.

ARCHEGONIA.—A few cells in the prothallial cushion soon become conspicuous by reason of their large nuclei. Each divides by two periclinal walls, forming a tier of three cells. The uppermost of these divides by two anticlinal walls at right angles to each other into four cells. These again, by periclinals, form the four cover and the four neck cells. The middle one of the original tier does not divide and becomes directly the single neck canal cell. The lowermost divides into the egg and the ventral canal cell (*figs. 29–32*). A suggestive irregularity sometimes occurs in the last mentioned division. The central cell, that is, the lowermost cell of the original tier, may divide in such fashion that the egg and its sister, the ventral canal cell, may lie side by side in the venter of the archegonium, instead of in the normal fashion of ventral canal cell above the egg (*fig. 32*). The cover cells project very little from the surface of the prothallium. Thus the archegonia are imbedded in the surrounding tissue, whose cells in immediate contact with the egg and the ventral canal cell become more or less modified in form. The neck canal cell pushes up like a wedge, spreads apart the four neck cells, and dissolves. The ventral canal cell also disappears (with a possible exception noted hereafter), and the egg lies free in the venter. There is a large receptive spot on the oosphere, and its nucleus is not centrally placed (*fig. 33*). I have never seen more than five archegonia in a single gametophyte.

FERTILIZATION.—Not only are the archegonia formed in the unshed spores, but frequently, at least, fertilization and the early phases of the sporophyte development take place while the sporangium with its prothallus are still in the strobilus. The strobili cease to grow, fade, and may separate from the plant before fertilization, but the spores do not fall from the sporangium. It was not until I had collected from the soil several hundred spores which had been shed, with the expectation of finding fertilization stages, that I thought to examine the withered strobili. Almost without exception in these I found embryos, whereas *in no case* have I found any evidence of fertilization in the spores that are shed.

FURTHER DEVELOPMENT OF THE MEGASPORANGIUM.—The glandular tapetum is very active until the megaspores have stored their maximum amount of nutriment for the growth of the embryo. At this stage they quite fill the sporangium cavity, which in consequence has assumed a four-lobed appearance. The tapetum then declines in importance. Its cells collapse and form a pavement-like layer. The outer layer of wall cells becomes greatly modified. In section it appears precisely like a similar section of the annulus of a leptosporangiate fern (*fig. 52*). Four areas of the larger thick-walled cells, corresponding to the protuberances caused by the spores lying within, are separated from one another by narrow strips of small cells with thin walls. The latter are the lines of dehiscence. The sporangium splits into two valves along these lines, but the halves do not separate so widely as to allow fertile spores to escape. Apparently they may open and close more than once. The sporangium appears fresh and active, and its wall contains chlorophyll until after fertilization has occurred. With the decline of the tapetum the lower stratum of the wall becomes more vigorous, as does a group of cells that lies just above the pedicel, and which projects into the sporangial cavity (*fig. 58*). This cushion is in close relation to the vascular strand and probably facilitates the supply of nutriment to the sporangium wall, until the embryos begin to form.

Frequently I have found microspores (in which the spermatozoids had formed) within the megasporangium at the period of fertilization, and it is possible that the microspores are hurled into a gaping megasporangium when ejected from the microsporangium.[1] This is rendered more probable by the frequent occurrence of microspores caught in the angles between sporophylls and stem. Moreover, if plants that have become somewhat dry be profusely watered, the mature microsporangia open explosively and discharge spores.

MICROSPORES.—The microspores of *S. apus* are much smaller than those of *S. Kraussiana* and *S. Martensii.* They early develop a pebbled, thick exospore, which causes much trouble in imbedding and sectioning (*fig. 69*). Moreover, a comparatively small number, in proportion to the immense output, mature. Curious aberrations in growth are constantly found. It was necessary to study mature gametophytes discharging spermatozoids and trace back the different stages to the mother cells. Frequent comparative measurements finally afforded a clew to detecting abnormalities in the early stages.

Not more than five sixths of the potential mother cells divide into spores; the others rapidly disappear. The division is accomplished in a manner analogous to the division of the megaspore mother cell, which is very little larger. Two spore coats develop, a thick spiny exospore, and the delicate membranaceous endospore. The microspores are shaped like the megaspores, but, unlike the latter, separate from one another as soon as the exospore develops. As was the case with the female gametophyte, the sexual generation begins before the microspore has ceased growing. At the moment that the microspores separate from one another, each possesses a thick and a thin coat, a layer of protoplasm parietally placed, with one nucleus, and a central cavity filled with fluid (*fig. 68*). The nucleus increases in size and divides. This process often takes place in that part of the spore where one of the lateral ridges meets the hemispherical base (*fig. 78*). The protoplasm increases in quantity and encroaches on the central vacuole. Granules of various sizes make their appearance in the cavity and in the surrounding protoplasm. These bodies stain precisely like the nuclei and the more regular ones may be mistaken for them, as I frequently discovered in the early period of my own work (*fig. 77*). By precautions in decolorizing, the presence of nucleoli always distinguish the nuclei from the granular masses. These bodies are formed by the agglomeration of many smaller granules. One of the nuclei formed by the first division remains against the wall. It may grow larger and the protoplasm immediately surrounding it is somewhat denser, but no wall separates it from the rest of the spore. This may be the vegetative prothallial cell (*figs. 70, 75*). The other nucleus passes into the center of the spore. The protoplasm that envelops it sends out radiating processes that incompletely divide the spore cavity into irregular chambers, each of which is filled with granular masses of various sizes and shapes (*figs. 76, 80, 81, 83*). These strands of protoplasm are continuous with a thin layer in contact with the endospore. The central nucleus with its envelope of protoplasm divides into two cells which usually separate from each other (*figs. 79–83*). By repeated division of each of these cells a complex results which consists of two uniform masses of sperm mother cells. There is no law of sequence which the cells follow in dividing, although the final product consists of cells very regularly arranged (*figs. 95–97*). The male gametophyte then is made up of one prothallial cell and a naked mass of sperm cells, which later come to float in the slime produced by the disorganization of the food granules. Sometimes at this stage the large deeply stained prothallial cell may be seen flattened against the endospore (*fig. 97*). There are about 128 sperm cells. The exospore splits along the three ridges from the apex downward, and the endospore, dilated with fluid, protrudes through the gap (*figs. 98, 99*). The sperm cells separate from one another, and a single spermatozoid is organized in each. These are spirally coiled like those of Osmunda—two complete turns and a part of a third—but I can demonstrate no cilia (*figs. 33, 100*). Neither in appearance nor in movement do they resemble any bryophyte spermatozoid with which I am familiar, or have seen figured. The movement of biciliate gametes is characteristically different from that of an ordinary fern. These spermatozoids progress with a screw-like motion. The latest stages of development occur in the strobili after they are shed.

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[1] I have examined *S. Martensii, S. Kraussiana,* and *S. denticulata,* growing in the greenhouse, with reference to this point. The two former do not shed their strobili, and I have found loose megaspores containing sporophytes in the soil on the benches where the plants are growing. The last mentioned species, on the other hand, sheds its strobili in profusion. I find, however, that their spores are invariably sterile and aborted, and therefore am unable to form an opinion as to whether this shedding is the normal habit, or due to cultivation in an unnatural environment.

MICROSPORANGIUM.—At maturity the microsporangium wall consists of two layers of cells, of which the outer is divided into regions of thick and thin-walled cells, which enable the sporangium to open lengthwise into two symmetrical valves (*fig. 62*). The microspores are discharged with much force. If plants that have become somewhat dry are watered copiously and covered with a bell jar, the ripe microsporangia burst open and jerk back their valves, which instantly recoil and hurl the microspores. These may be seen, looking like red powder, lodged in the axils of leaves or upon any other part of the plant where they have chanced to fall. Of necessity the waste must be great. If this is the method adopted by the plant to secure fertilization it may account in a measure for the extremely small number of sporophytes that are developed.

S. apus grows most profusely in a neighboring locality, where almost daily observations have been made during the past year. Early in May 1900, when this work was undertaken, the strobili were well advanced. It was observed that if several eggs in one strobilus are fertilized, the formation of new sporangia is checked. The sporophylls begin to decay, as finally does the axis immediately below the fruiting head. The production of new strobili went on until late in August, at which time all the strobili were shed, whether fertilized or not. In September vigorous vegetative growth took place during the fall rains, and continued until checked by several days of very cold weather in December. In the latter part of the same month, upon removing the snow that covered the plants to a depth of six inches, they were found to be green and ready to grow at any favorable moment. Large sods were lifted, without disturbing the plants, and brought into the warmth of the greenhouse, whereupon they responded promptly to the blander conditions. After a week, upon gently disentangling the individuals in order not to detach the semi-decayed strobili which were partially covered by the soil, I found several young sporophytes which had thrust their cotyledons and roots through the crevices of the megasporangia. From this it seems safe to assume that an embryo may have two periods of growth separated by one of quiescence, quite comparable to those of seed plants.

SELAGINELLA RUPESTRIS.

There could be hardly a more striking contrast in the external appearance of two closely related plants than exists between these two species of Selaginella that are natives of New England. *S. rupestris* is to be found in the most exposed situations, growing on the granite rocks on the mountain sides, wherever there has been enough weathering to insure the deposition of a little soil in the hollows. For six months of the year they endure alternate drought and drenching, and the frequent and rapid changes of temperature which are characteristic of this region, with no more protection than is afforded by their own structural adaptations. The midsummer conditions are even more trying. The plants that were studied for this work grew on bare rocks upon which the sun beats nearly all day from June to September. The fruiting spikes are to be found in profusion at all times of the year, but, as will develop later, the spores in the main are sterile. Material was fixed first about June 15, 1900, and at intervals of two weeks thereafter until February 1901. Sods were lifted from the rocks, and planted in shallow boxes which were kept in a warm place exposed to the direct sunlight. The spores were shed freely all summer. I collected other plants from a similar xerophytic situation at Starved rock, Illinois, in August, and for comparison material was sent me in Northampton, Mass., from Austin, Texas, in November. These three regions are 800, 900, and 1600 miles apart. The plants collected in Massachusetts and Illinois, from June until February, almost without exception produced megasporangia only. The Texas material collected in November, on the other hand, was almost purely microsporangiate.[2] Expecting to find prothallia and young sporophytes developing in the spores that had been shed, these were picked out from the loam from which the plants were growing and killed at frequent intervals during the summer, with the purpose of getting all important stages. In all cases these proved to be barren. Late in August—as was the case with *S. apus*—the young sporophytes were discovered protruding from a withered strobilus that was nearly covered by the dirt. Further search produced many well-developed embryos, but it was apparently too late in the season to secure early stages (*fig. 126*).

During the first week in January, a sudden thaw was succeeded by several days of rain. Plants were collected from the mountain and gradually brought into a greenhouse temperature. The old strobili became greener at their tips, and new vegetative shoots started from the lower part of the stems. It is doubtful whether the increase in the number of individual plants in a given locality is due to any considerable extent to sexual reproduction. A hollow in the rock, or a crevice, becomes filled with a closely compacted colony that is the result in great measure of vegetative reproduction, where prostrate branches, under favorable conditions of moisture, have rooted, and later have severed their connection with the parent plant. In examining many colonies, very few young plants that originate from spores are in evidence, although the soil may be thickly beset with the spores that have been shed. Bits of the old plants that have been torn off by the action of the wind or rain are frequently caught in crevices along the precipices, and it is from these that new clumps are most frequently started.

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[2] Some of the Texas material was submitted to Professor L. M. Underwood, of Columbia University, for identification. He informs me that it is not *S. rupestris*, but a closely allied unnamed species.

In *fig. 124* I have endeavored to convey an idea of the structural adaptation of the strobilus to its austere environment. The closely overlapping sporophylls form four rows, in whose axils the sporangia have little space to develop. The growing apex is protected by at least twelve and frequently sixteen sporophylls which envelop it. The epidermis is two or three layers of cells thick on both surfaces of the sporophyll, except in a shallow groove running lengthwise along the middle of the ventral surface. In this groove are the comparatively large crowded stomata, which are protected by the next older overlapping sporophyll of the same row. While the leaves are yet very small the apex ceases to grow and becomes transformed into a branched spine. The formation of the horny epidermis proceeds from the apex toward the base. Between the ligule and the sporangium the tissue retains its meristematic nature. The vascular bundle occupies the central shaft of the strobilus, and is augmented from the apex downward by the leaf traces that join it from the sporophylls. Four large communicating air spaces, spanned by trabeculae, surround the entire system. These communicate with the exterior by certain larger chambers into which the stomata open. There is little closely compacted tissue in either sporophyll or stem. All the cells except the epidermis and the vessels contain chlorophyll. This structure is in marked contrast to the delicate unprotected sporophylls of *S. apus*.

A single superficial cell, which uniformly is so close to the base of the subtending sporophyll that it is impossible to determine whether it belongs to the stem or the leaf, is the origin of the sporangium (*fig. 101*). The sporophyll immediately above it starts simultaneously from an exactly similar cell. A wall separates the archesporial cell into an epidermal cap cell and a hypodermal cell (*fig. 102*). The sporangium wall develops from the former, the sporogenous tissue from the latter. A few sporogenous cells near the base originate from the stem tissue (*fig. 105*).

The tapetum and sporangium development are quite like those of *S. apus*. The sporophylls and stem apex, on the other hand, have no apical cell. The ligule appears later in the history of the sporophyll than in *S. apus*, and the megaspore mother cell is somewhat larger. Certain cytological features serve to distinguish these cells from the sterile sporogenous cells (*fig. 106*). The division into spores presents some curious variations. Sometimes the spore mother cell divides once only, forming two megaspores; again, after the first division, one of the daughter nuclei may divide, or occasionally both. In any case, so far as observed, but one or two normal megaspores are ever formed; if there are others, they are dwarfed in size and never grow. That the exospore is a membrane common to both spores is evident from *figs. 119, 120, 121*. The formation of the mesospore and endospore is not preceded by any such deeply staining layer as is represented in *fig. 42*. The protoplasmic vesicle expands and overtakes the spore wall. This stage terminates the development of the megaspore (*fig. 123*). In the older sporangia, nearer the base of the strobilus in the specimens that I examined, no further development had occurred beyond increase in size and thickness of the spore coats — the contents showed that the spores were abnormal.

This sequence of events, although followed step by step repeatedly, had been rejected as probably not normal, until the sporophytes were discovered. As the number and shape of the megaspores in these sporangia which contained embryos agree with the stages described, in spite of the gap that remains to be bridged between the megaspore and mature gametophyte, it seems reasonable that the observations can be relied upon as far as they go (*figs. 108-120*). A very close series of stages from start to finish is necessary to produce confidence in any interpretation of phases of a plant which displays so many irregularities, and evidently has so nearly lost its power of sexual reproduction.

The development of the microspores has not yet been followed in detail. Observations on this subject, together with the growth of the female gametophyte and the embryology, will be given in a future paper. One interesting feature that may be noted now is the incomplete septum which projects into the cavity of the microsporangium (*fig. 125*). This is formed in part from sterilized sporogenous tissue and in part from the cells of the pedicel.

Since the above was written, a package of fresh material has been sent me from Texas. All the plants have begun their spring growth and the winter strobili are growing at the apex. The first sporophylls of the season subtend megasporangia. I find not more than eight or ten in each strobilus. Above these are microsporangia to the number of twenty or thirty. In this material it has been my good fortune to observe the method by which the spermatozoids obtain their entrance to the megasporangia. A perfectly fresh, vigorous strobilus was cut from the plant and stripped of its sporophylls, thus exposing the sporangia *in situ*. A megasporangium, which was observed gaping open and in close proximity to a microsporangium that had discharged its microspores, was separated from the strobilus and examined under the microscope. Six microspores were caught on the sculptured surface of the megasporangium near the edge of the valves, which were slightly separated from each other. One microspore, evidently mature from the fact that the exospore was split and the endospore protruding, suddenly discharged a current of slime which at first proceeded directly away from the megasporangium. Soon, however, as if acted upon by some attractive influence from the gametophytes within, the stream turned abruptly and entered the opening between the megasporangium valves. The spermatozoids were swimming with characteristic rotary motion in this stream. With difficulty, it was possible to make out that they were similar in shape to those of *S. apus*, but much smaller. To each was attached a vesicle. An attempt to stain them with osmic acid on the slide failed to demonstrate any more details.

ADDENDUM.—Since the foregoing was forwarded for publication it has been possible to verify the main facts and to explain certain apparently contradictory features with regard to *S. rupestris*. The spring and early summer of 1901 were extremely wet as compared with those seasons in 1900. *S. apus* growing in low pastures made few strobili and aborted spores in contrast to the profusion of the year before, whereas *S. rupestris* throve in the unusual supply of moisture and developed strobili, which in turn produced embryos prodigally. The impotency of the megaspores gathered in midsummer of 1900 was obviously due to the lack of water; for at the expiration of the rainy season this year, the last of June, and before the plants had suffered from drouth, they were lifted with all the underlying humus and placed in an open situation in the Botanic Garden. Profuse watering was continued and thorough draining secured. A large percentage of the strobili ripened after fertilization had occurred, and instead of few embryos found with much effort as in the season of 1900, hundreds of young sporophytes have been secured. The sequence of events in a propitious season, based upon the observation of two years, seems in brief to be this: Strobili are formed on the new vegetative shoots of the plant in late summer and autumn. Only megasporangia develop that season, and in these the gametophytes reached the stage bearing archegonia. In the spring, these strobili resume their apical growth, and first microsporangia appear. Thus each strobilus has a basal zone of megasporangia approximately six months old, and above it a narrow region of microsporangia. The number of microsporangia appears to be strictly limited. I have found eight to twelve as a rule. Thenceforth so long as the strobilus continues to grow during the remainder of that season megasporangia only are developed. The production of these is checked in case embryos form in the lowermost zone of

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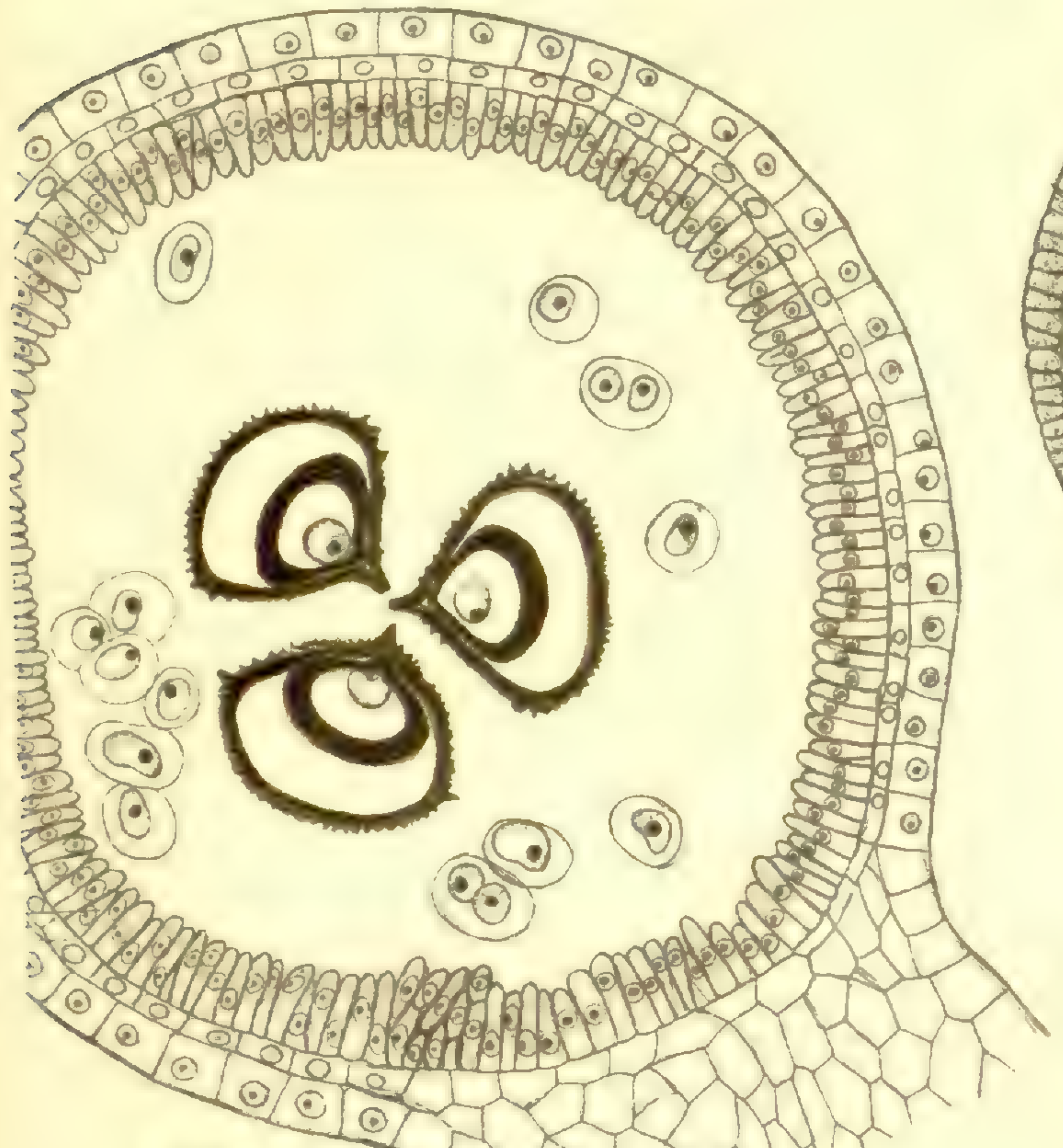

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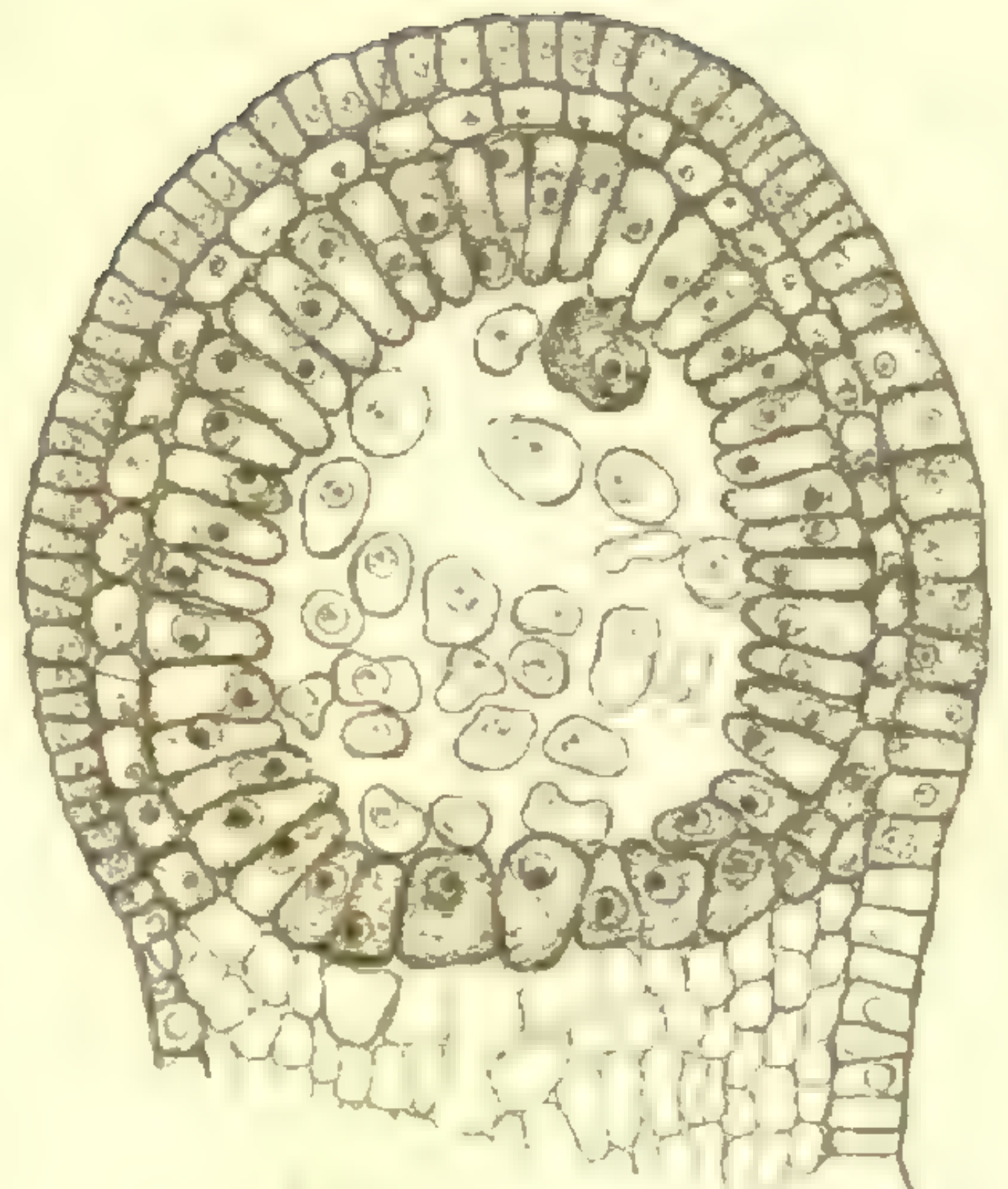

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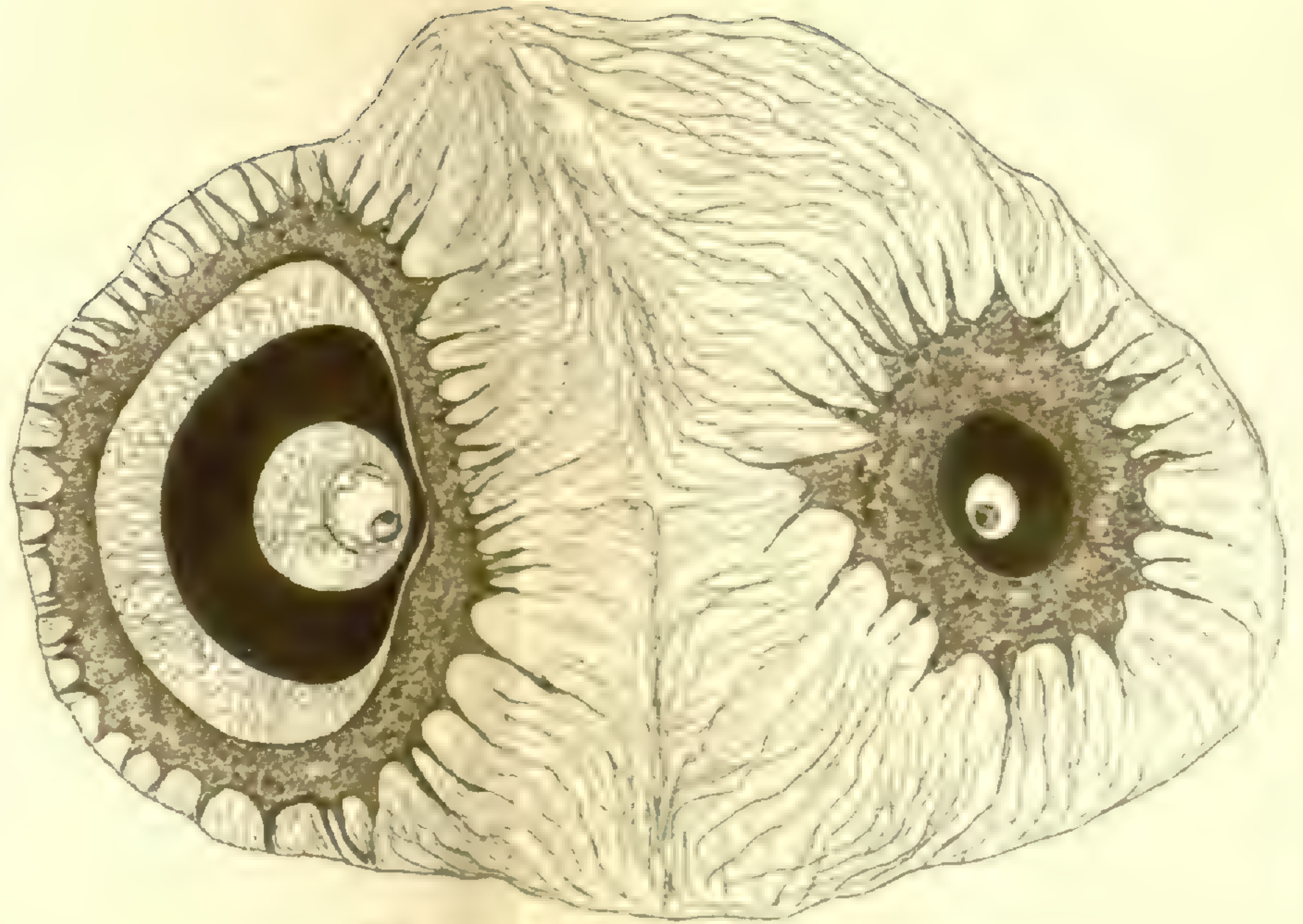

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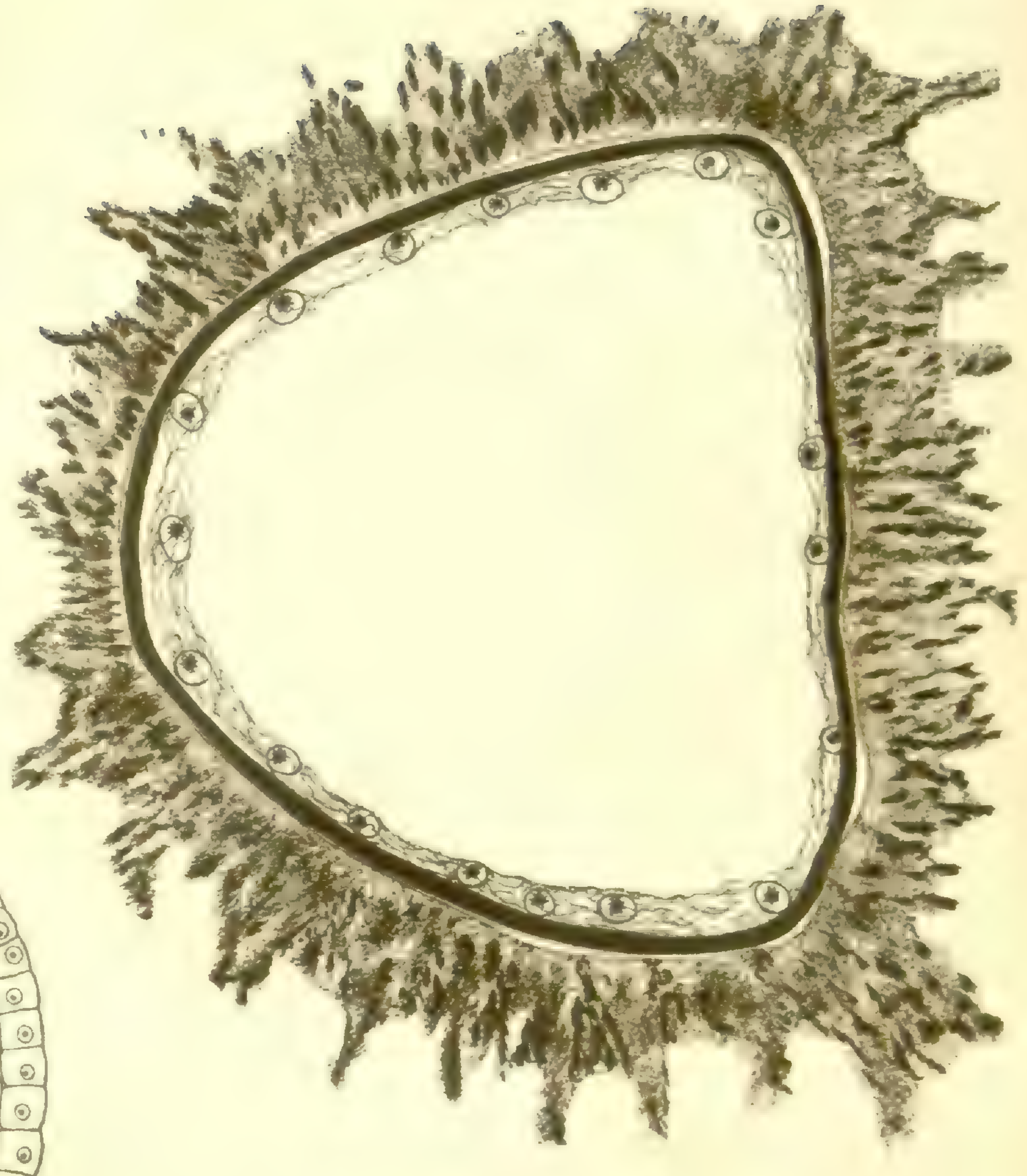

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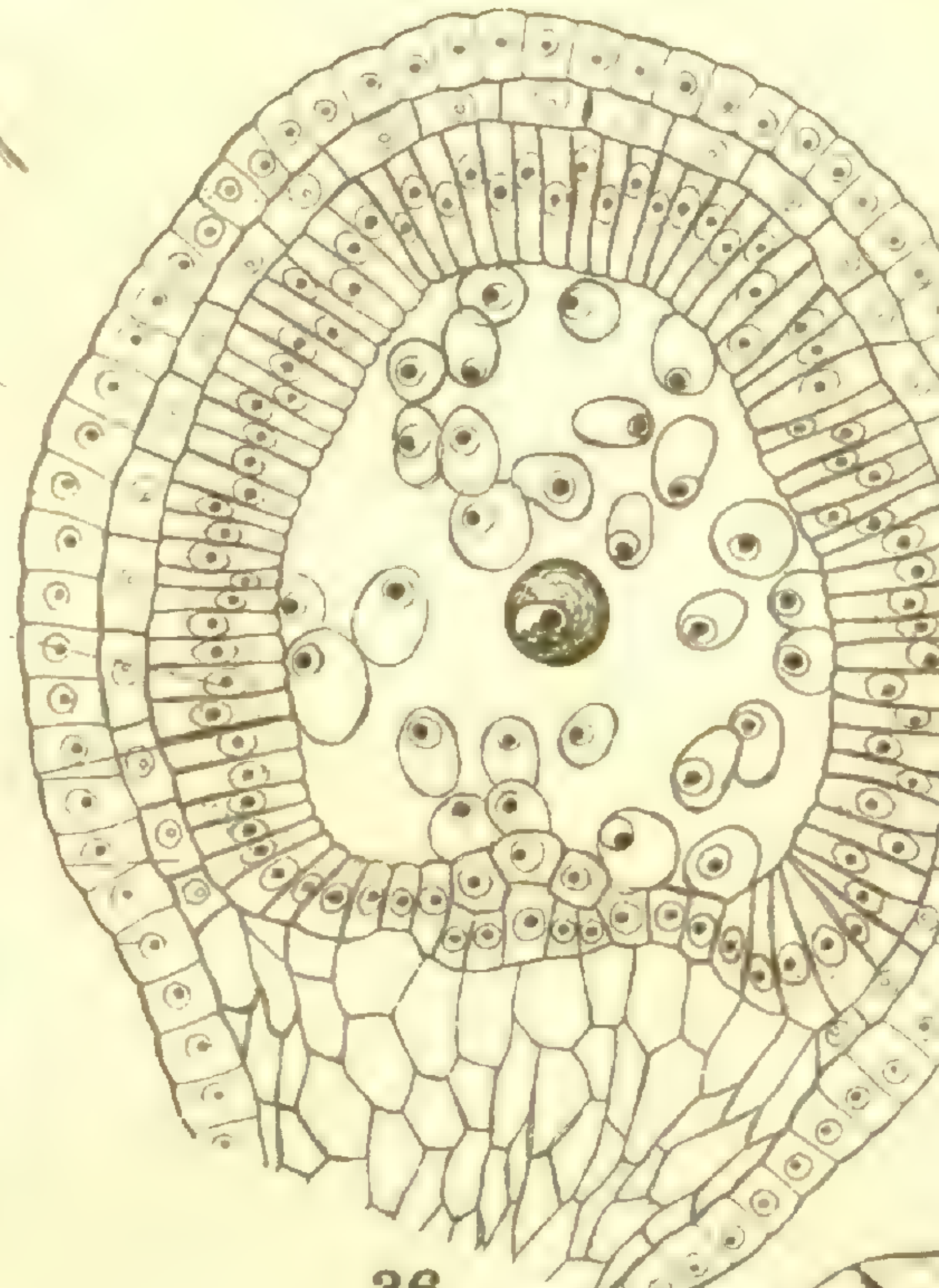

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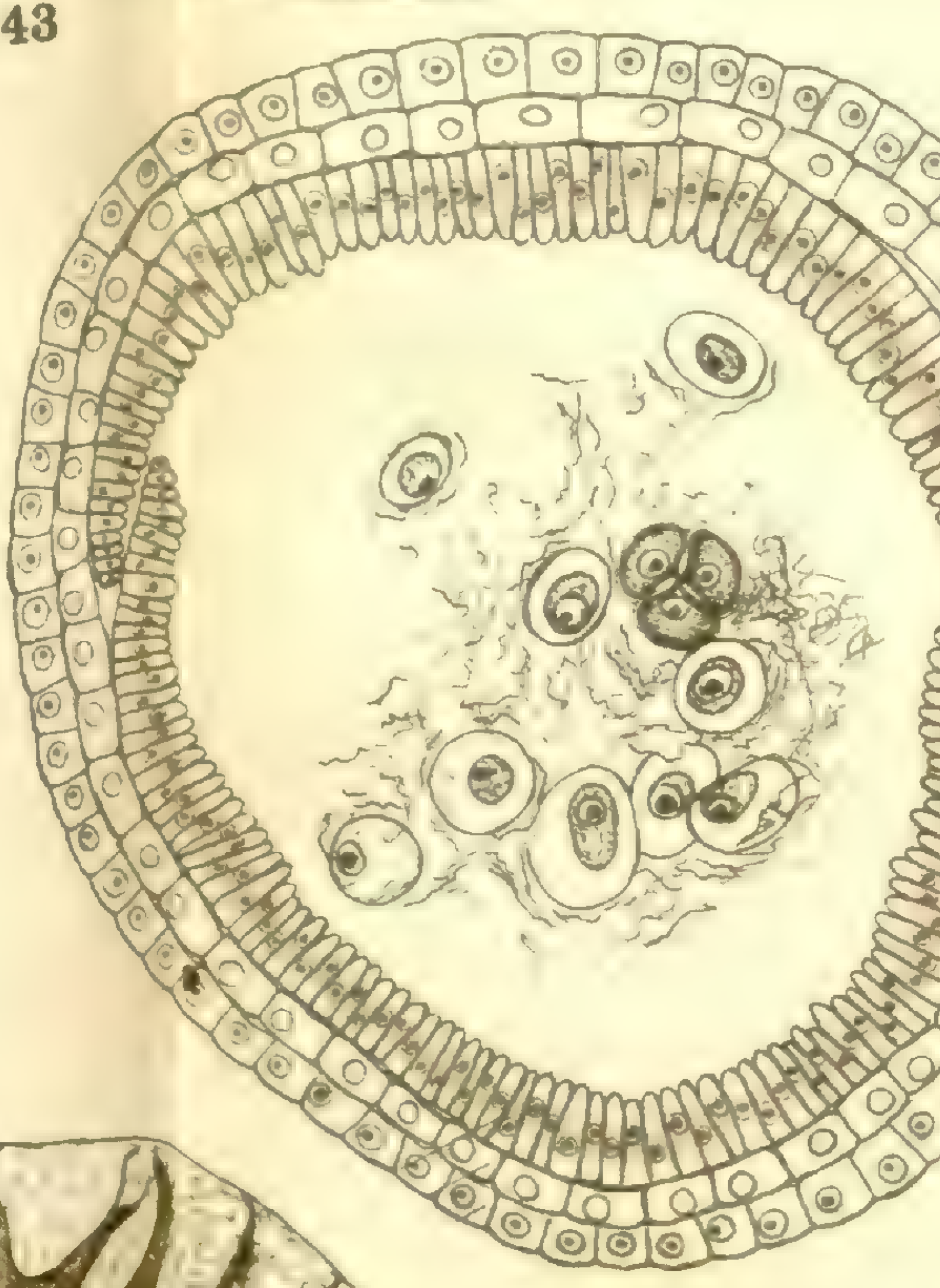

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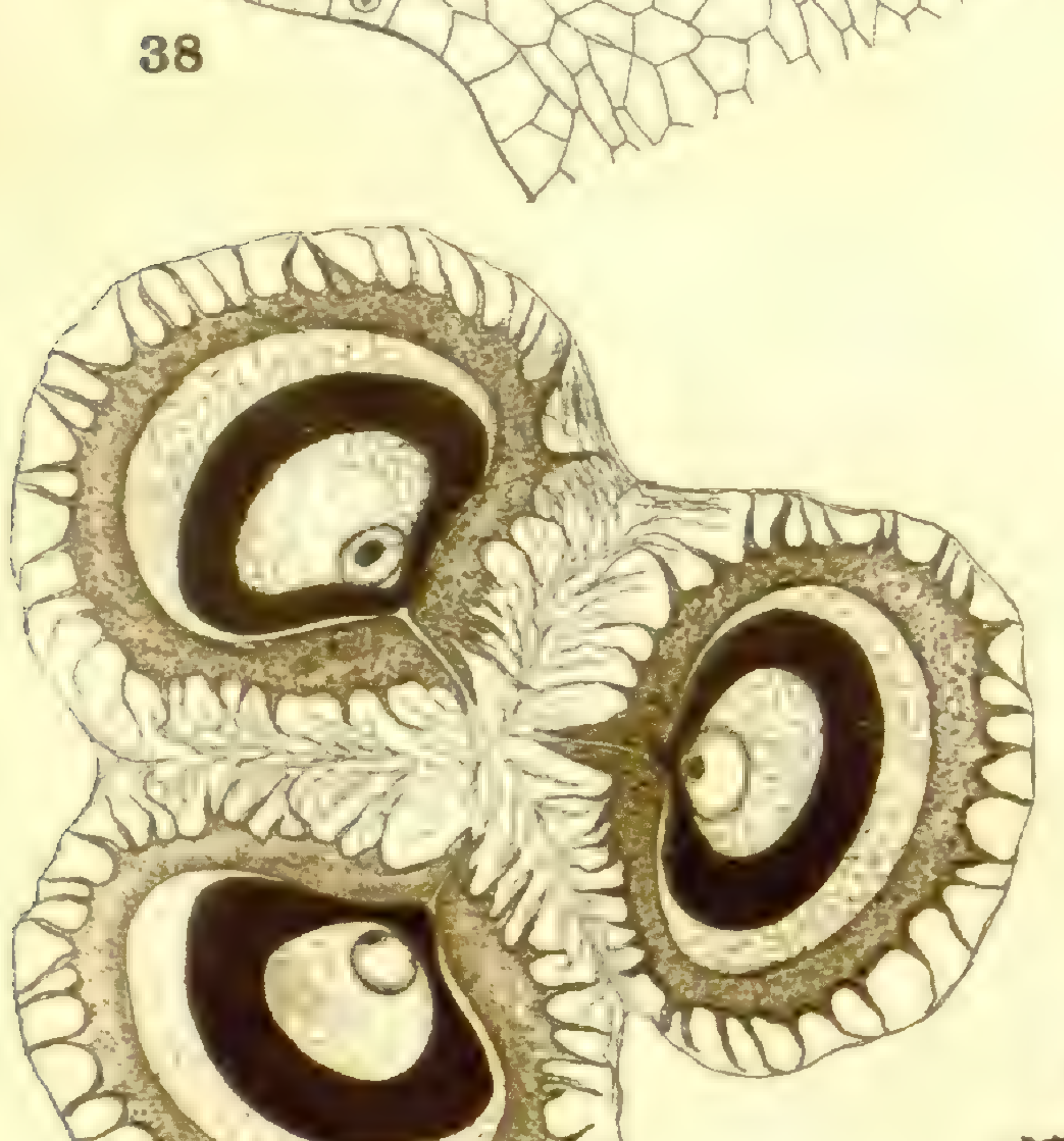

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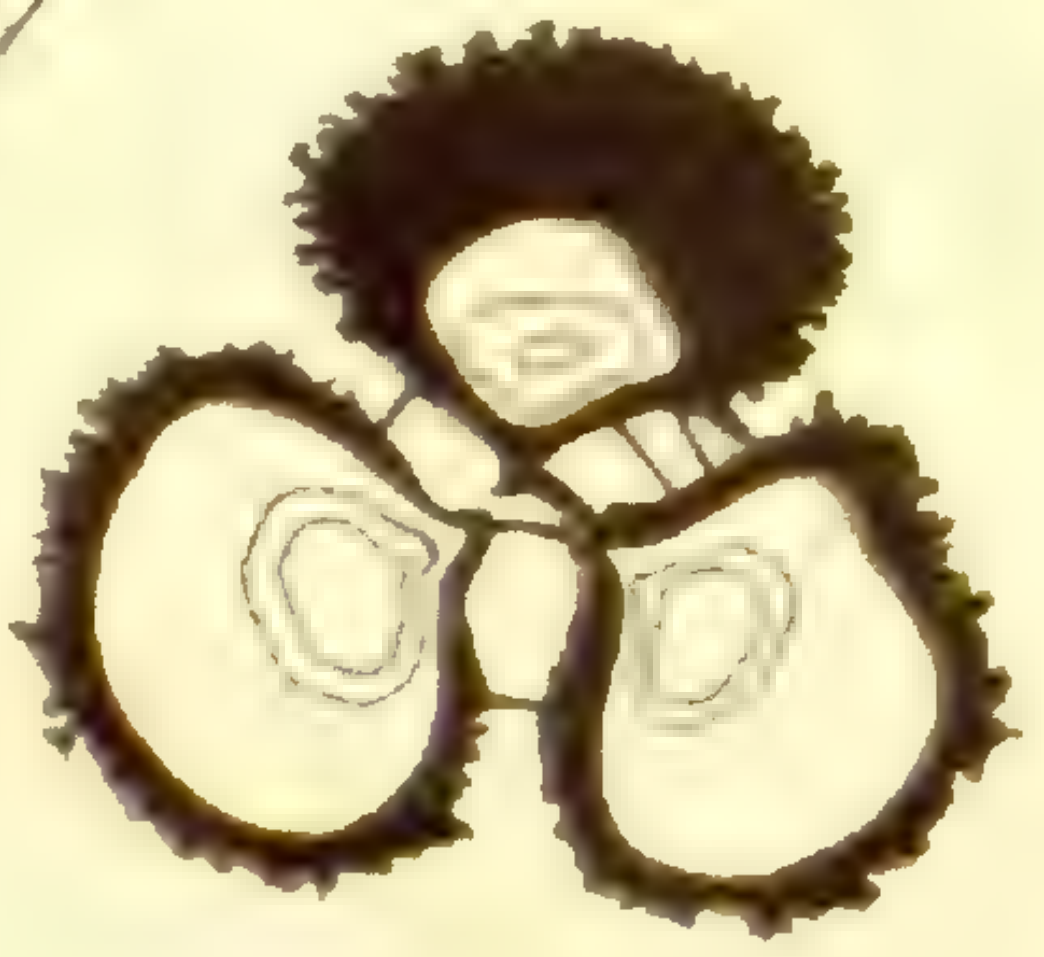

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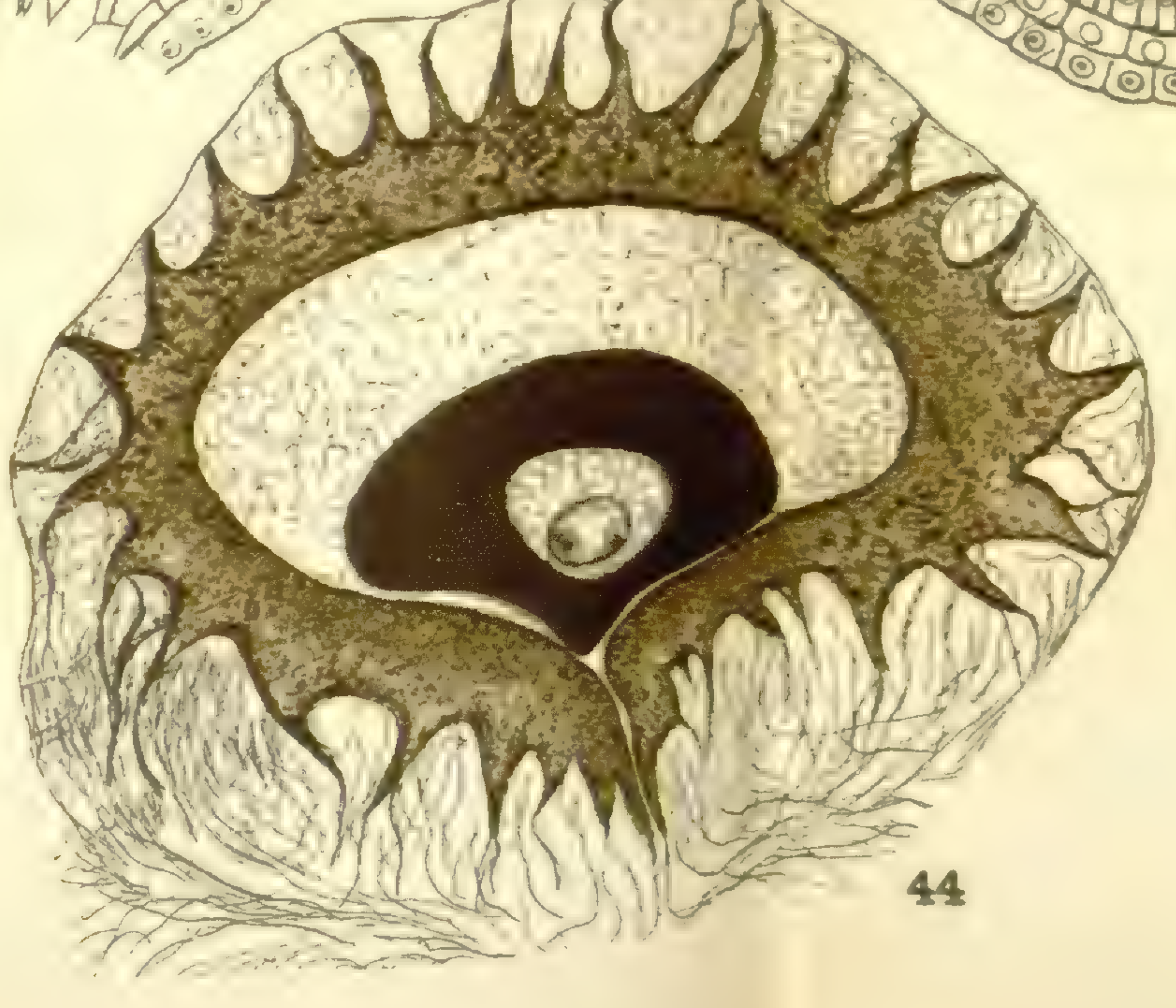

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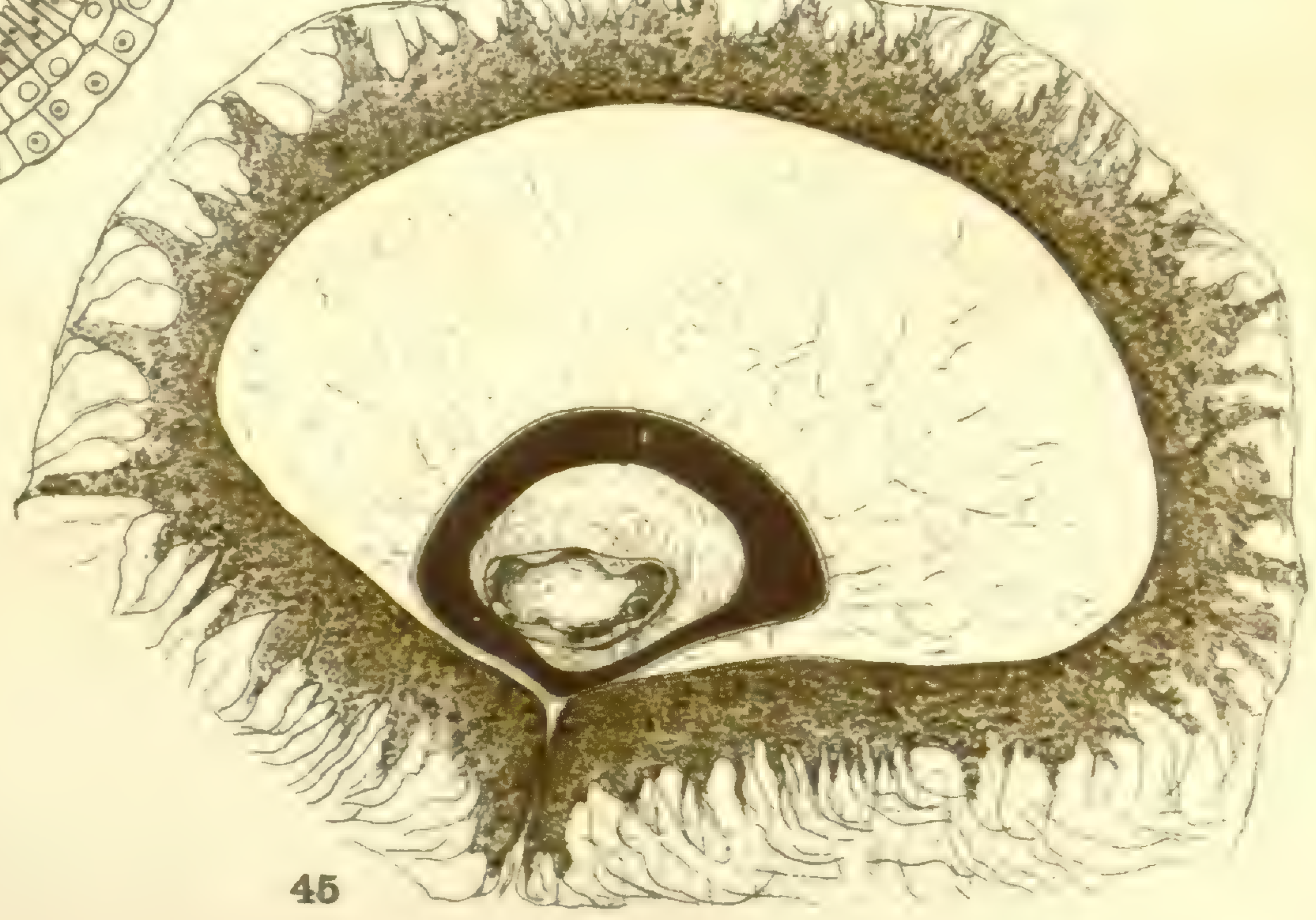

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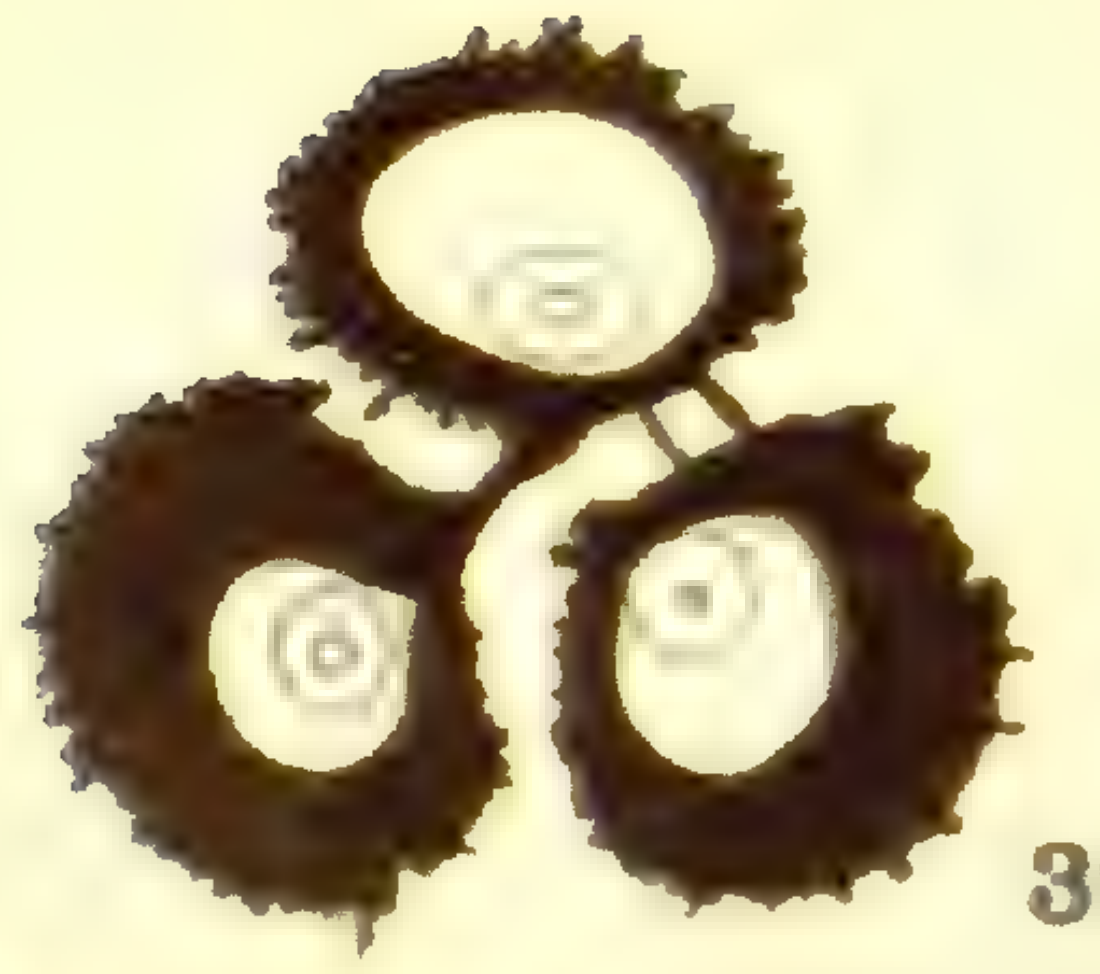

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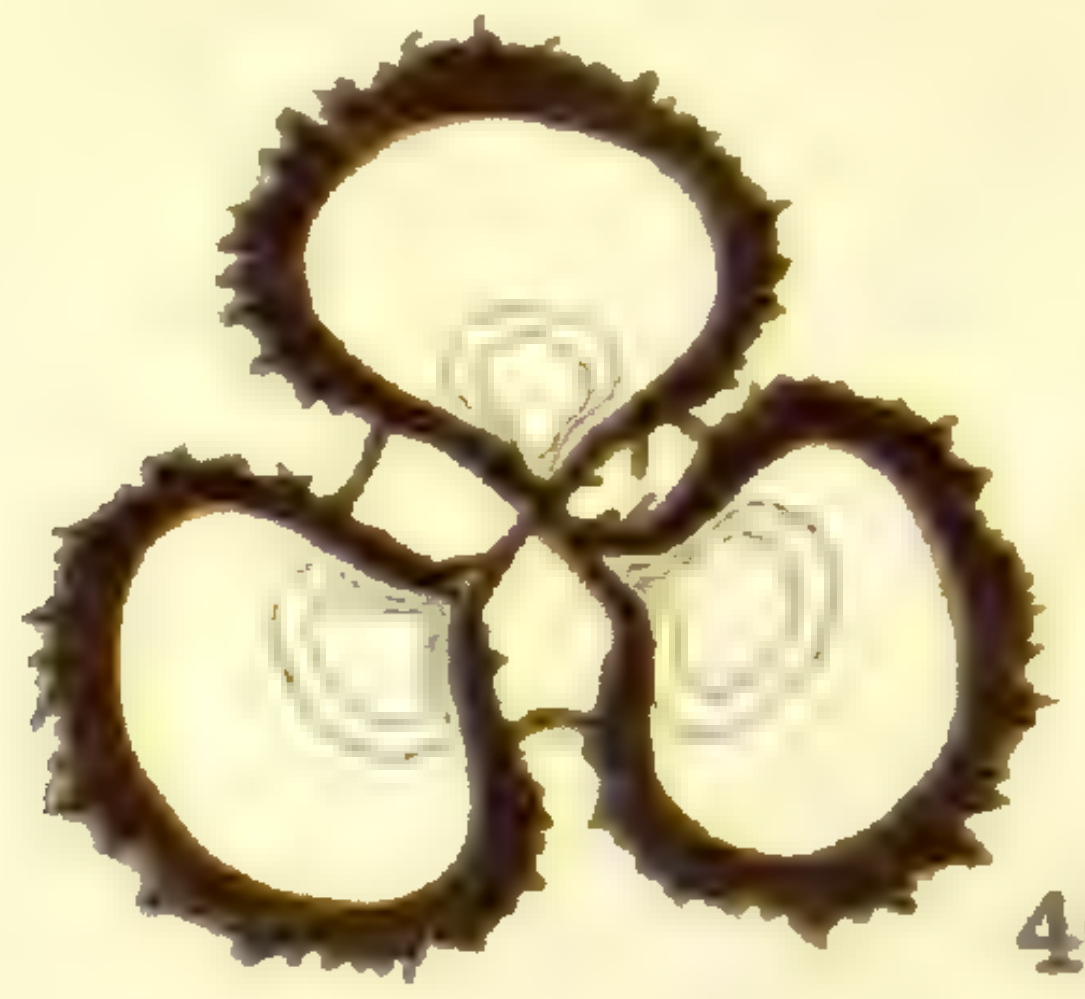

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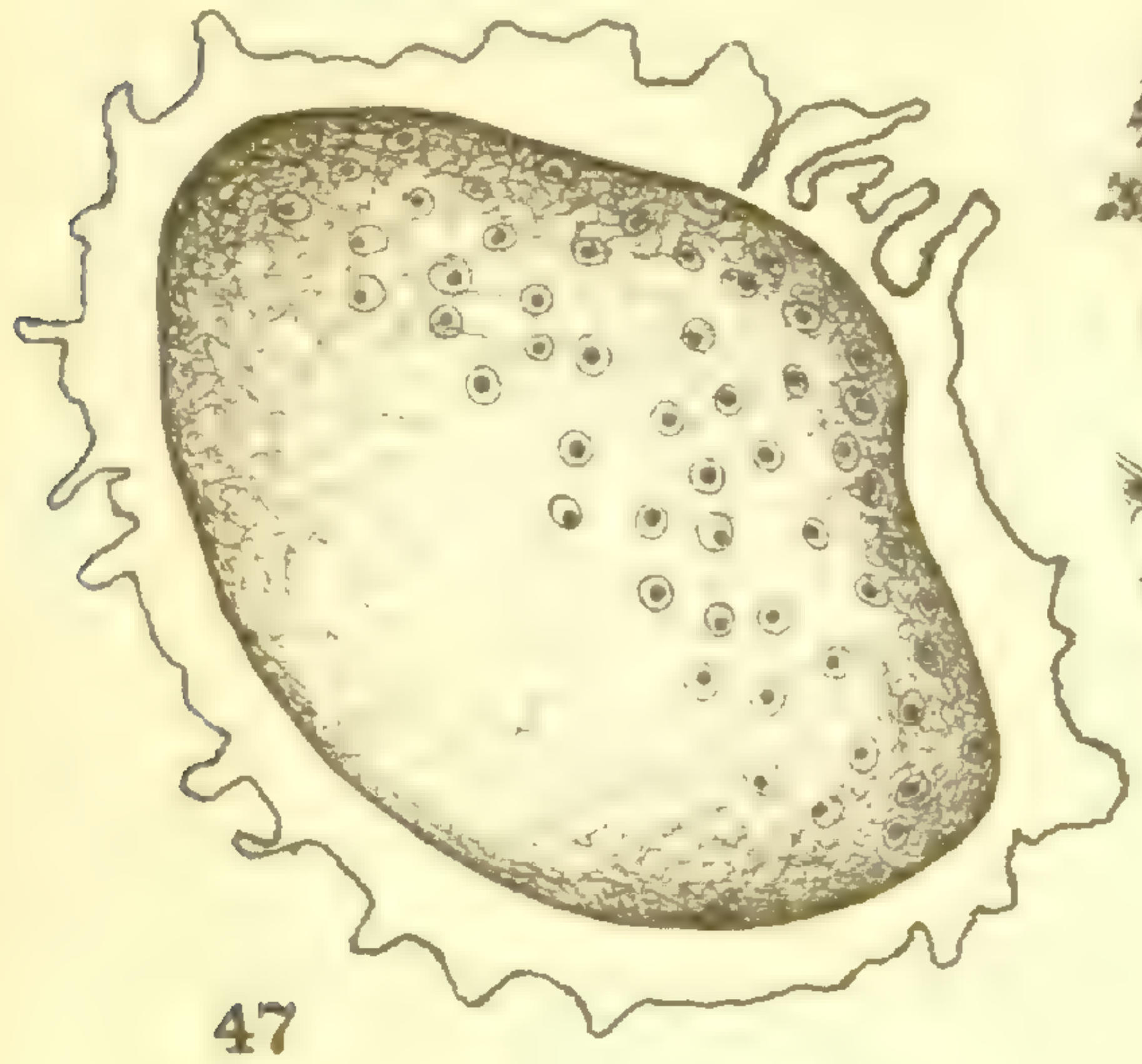
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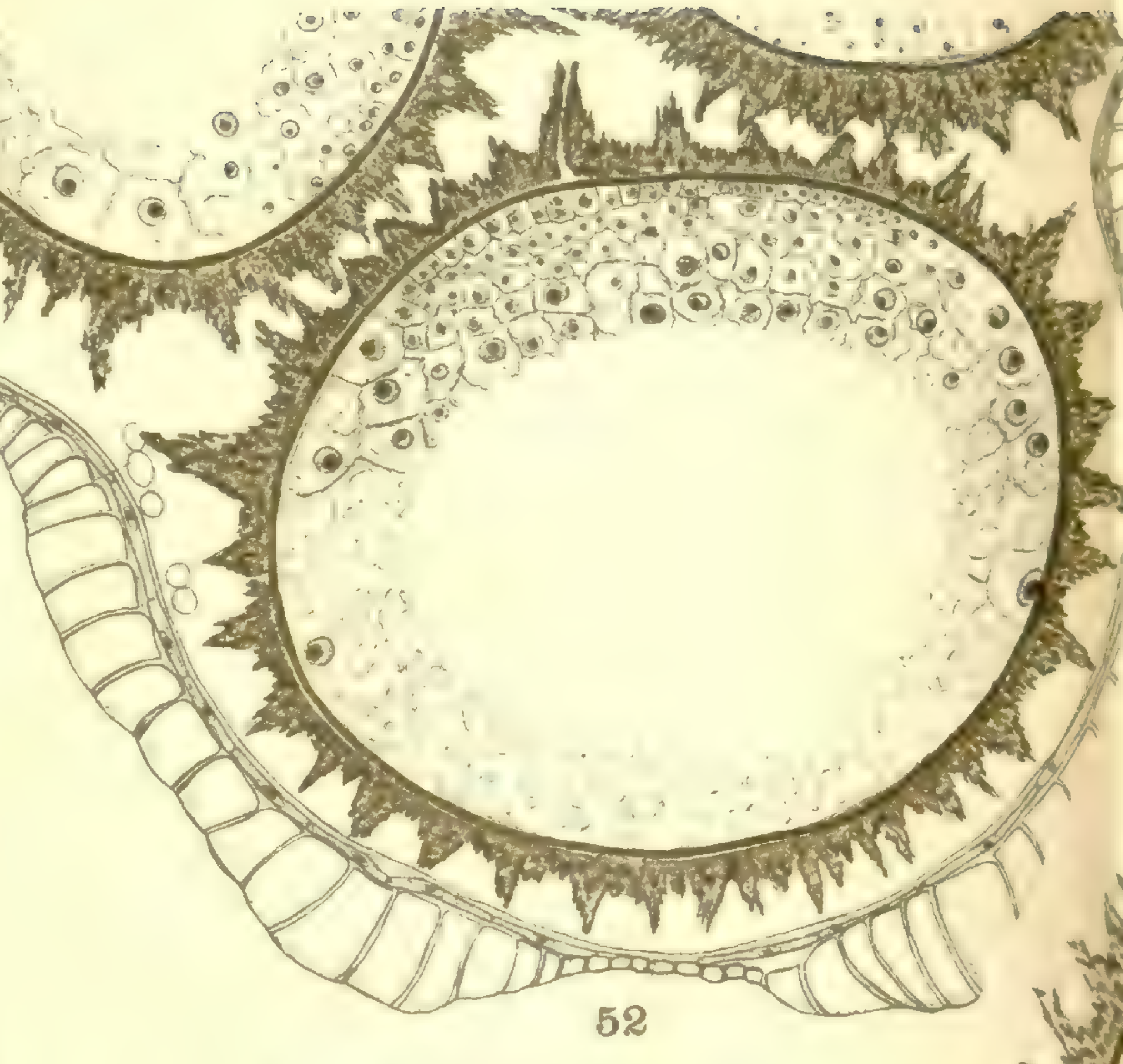
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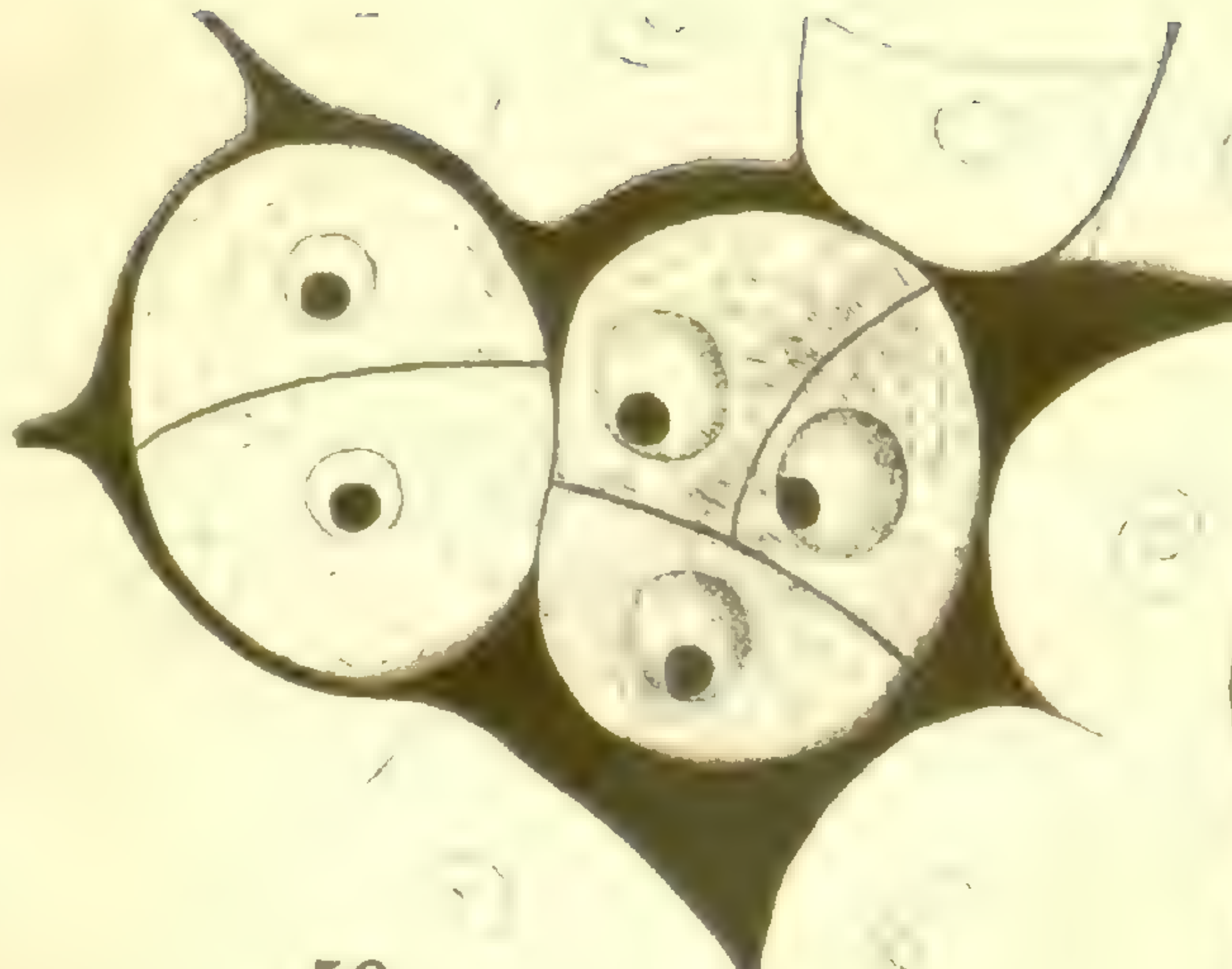
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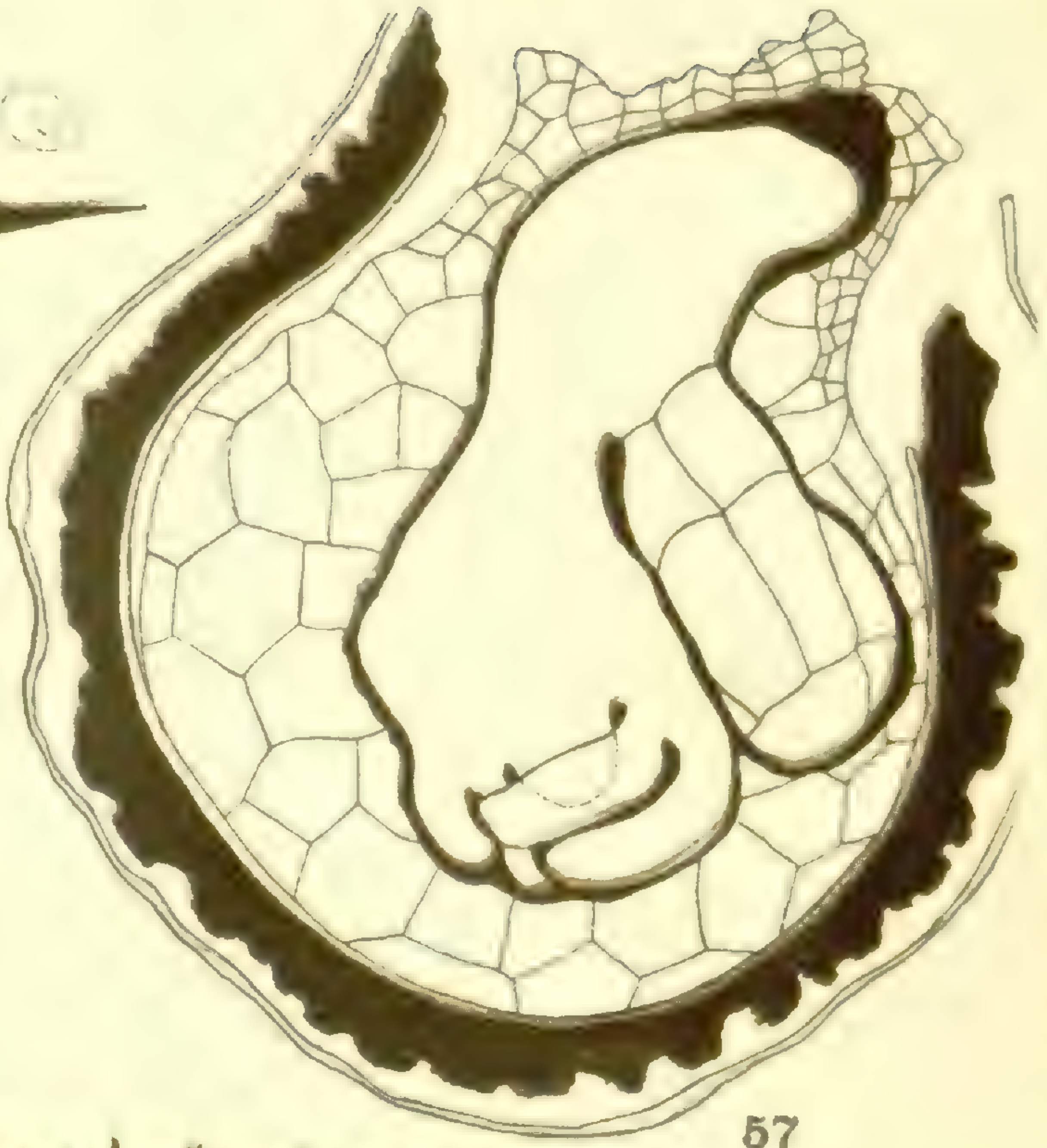
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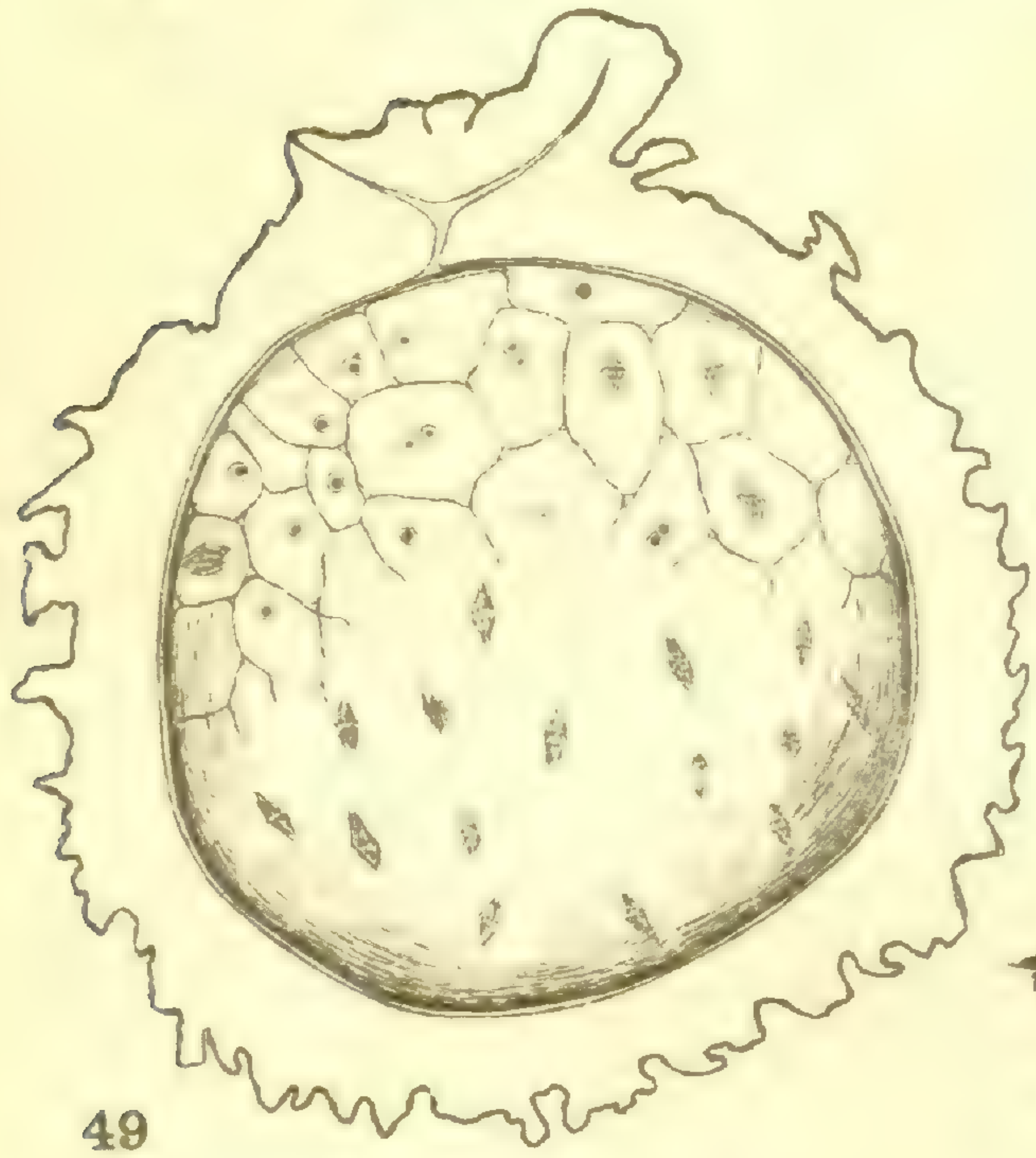
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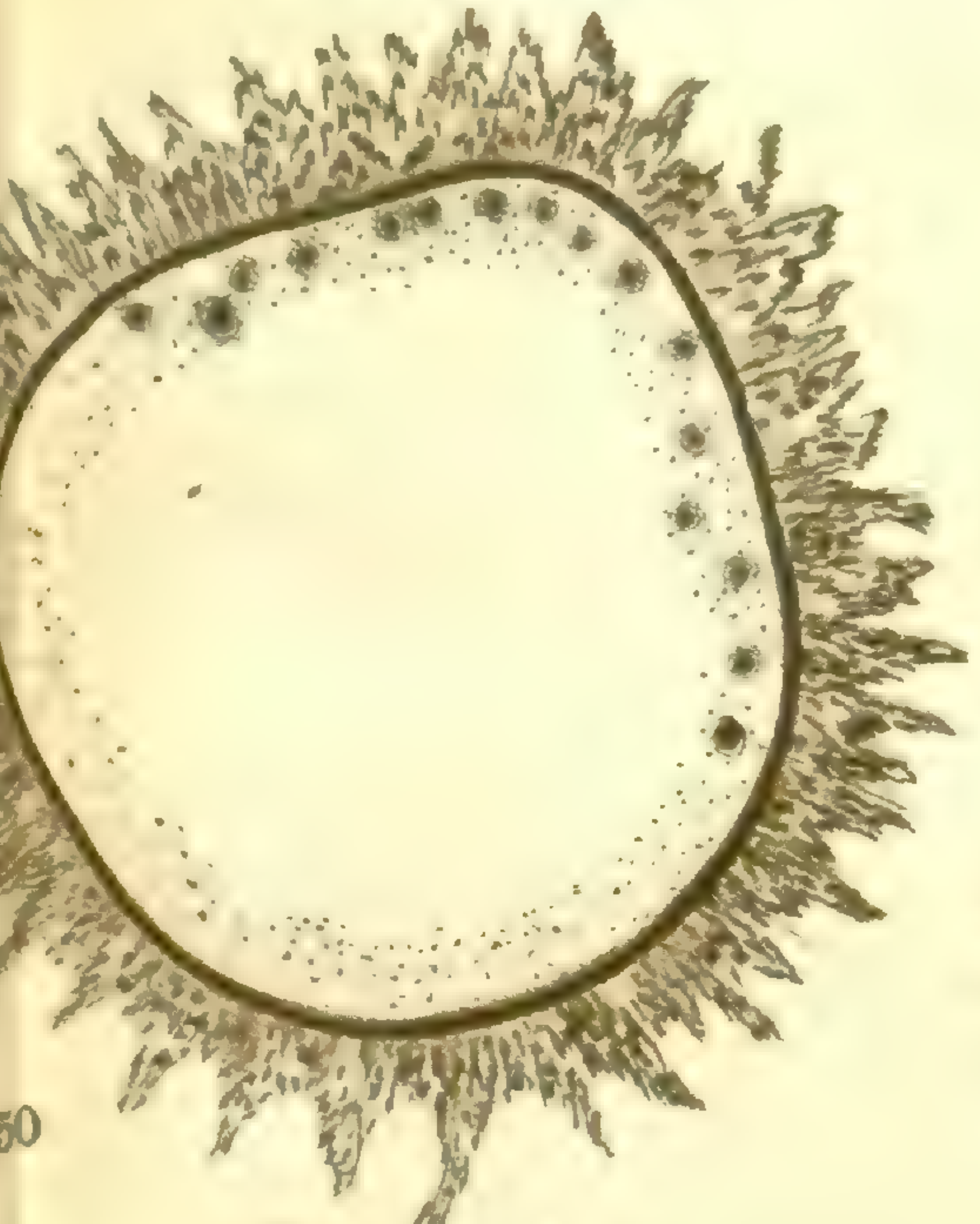
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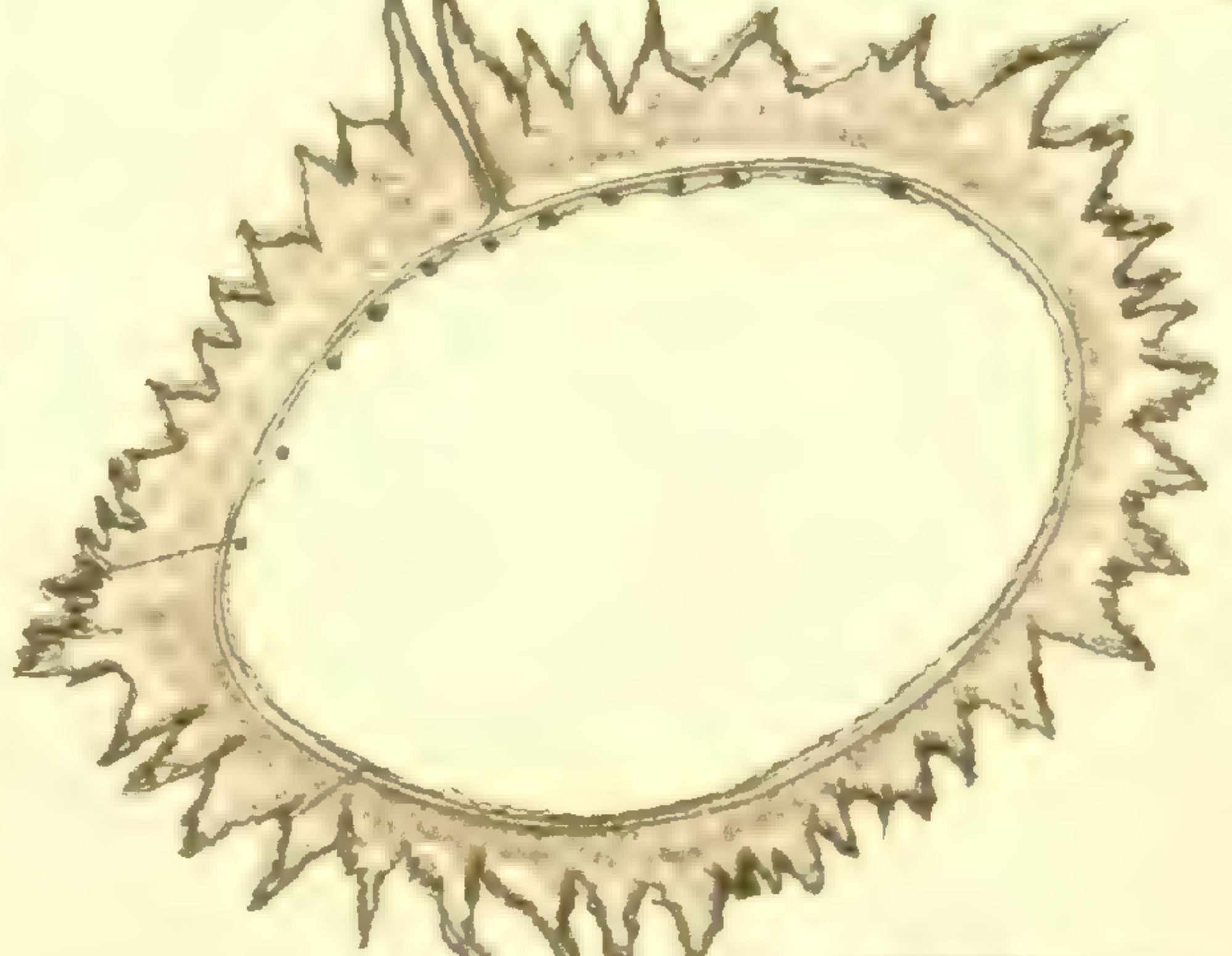
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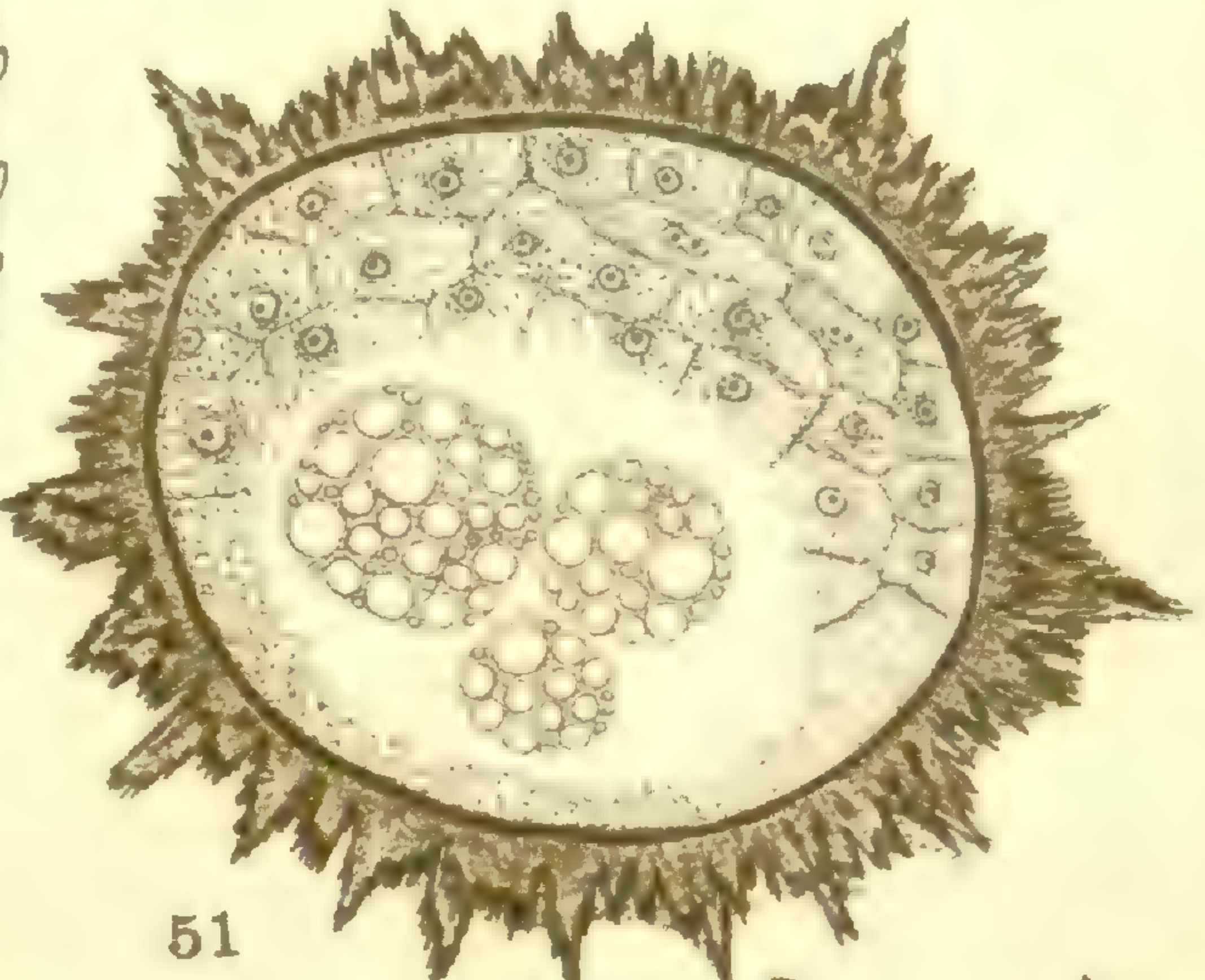
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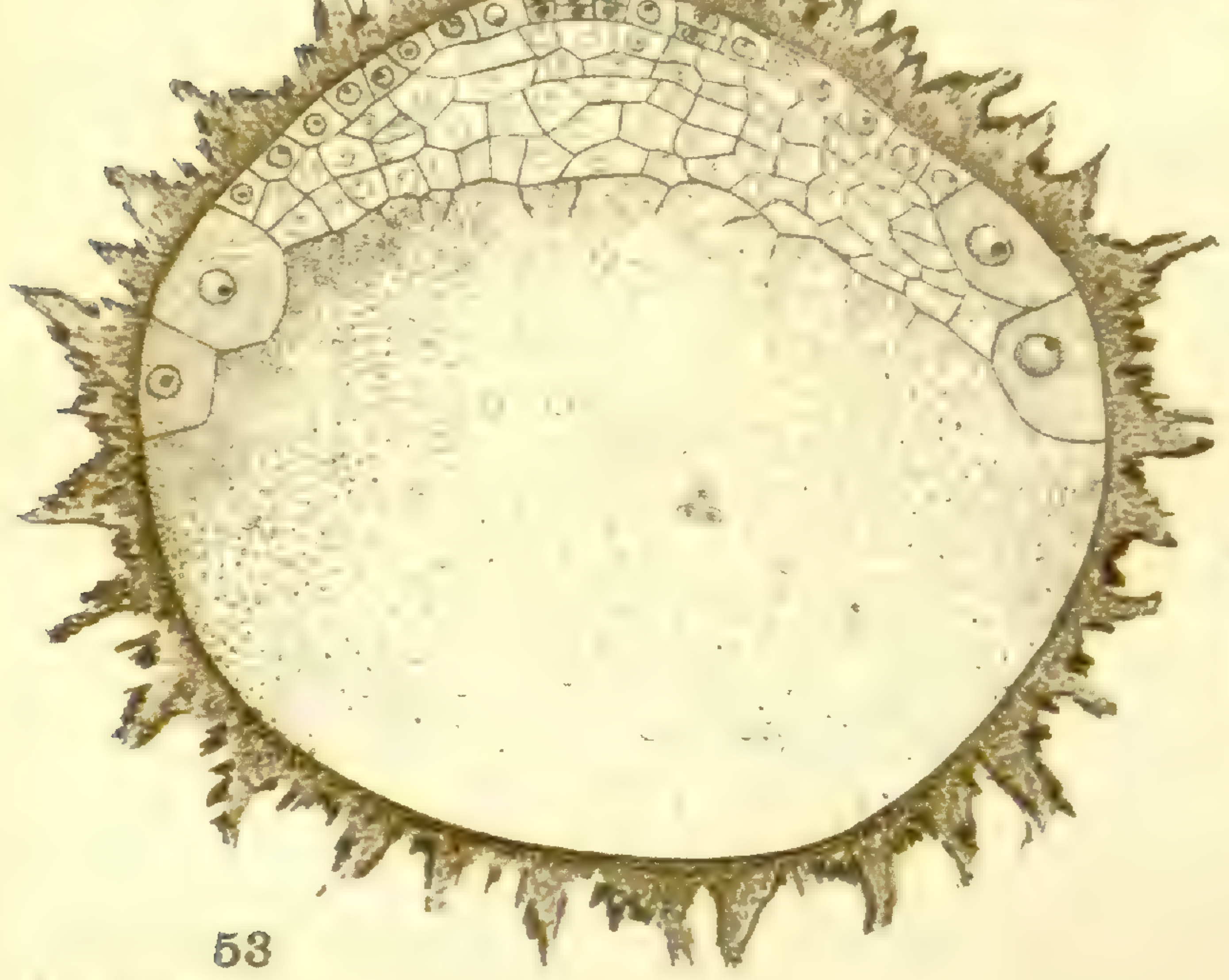
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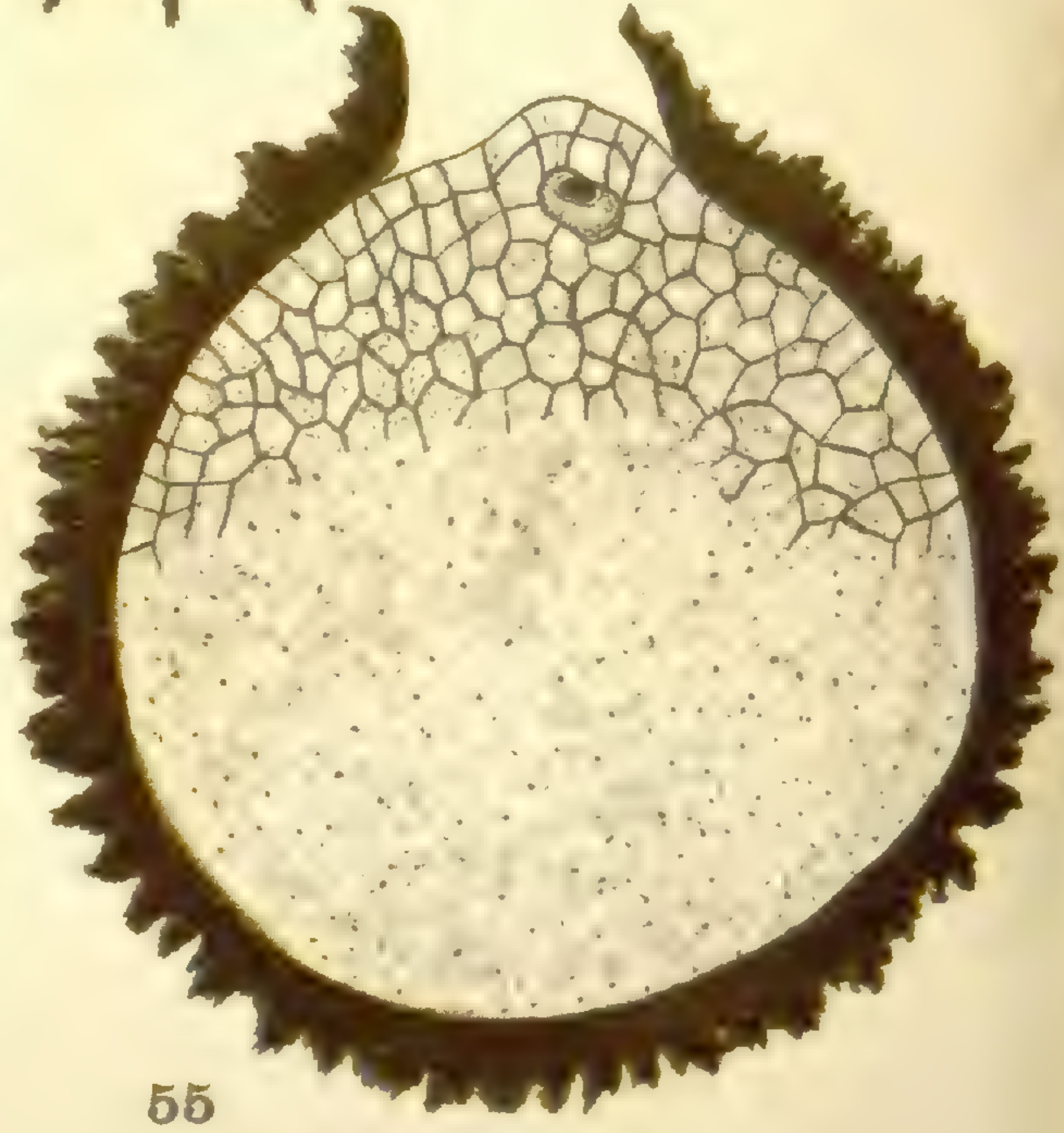
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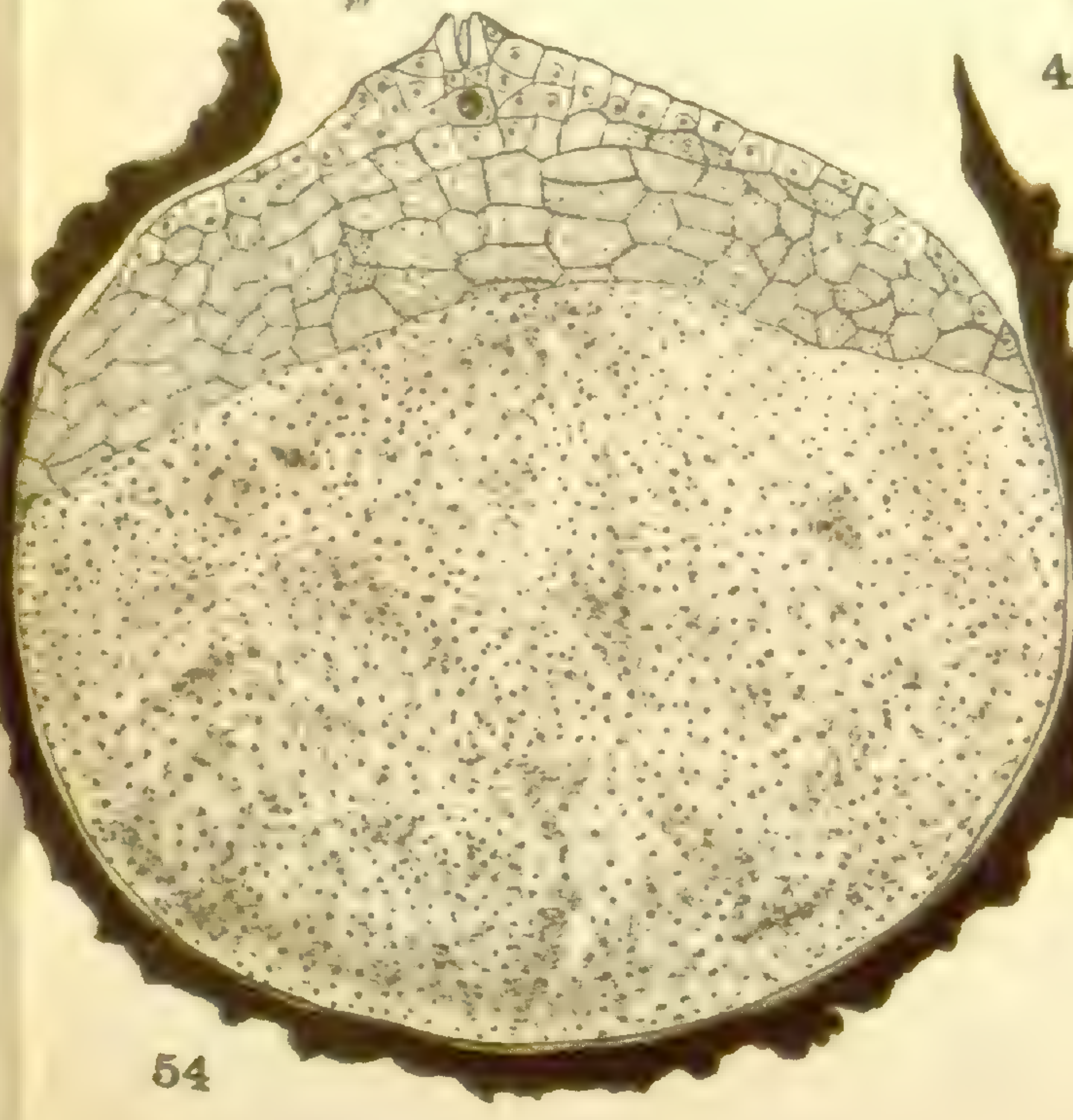
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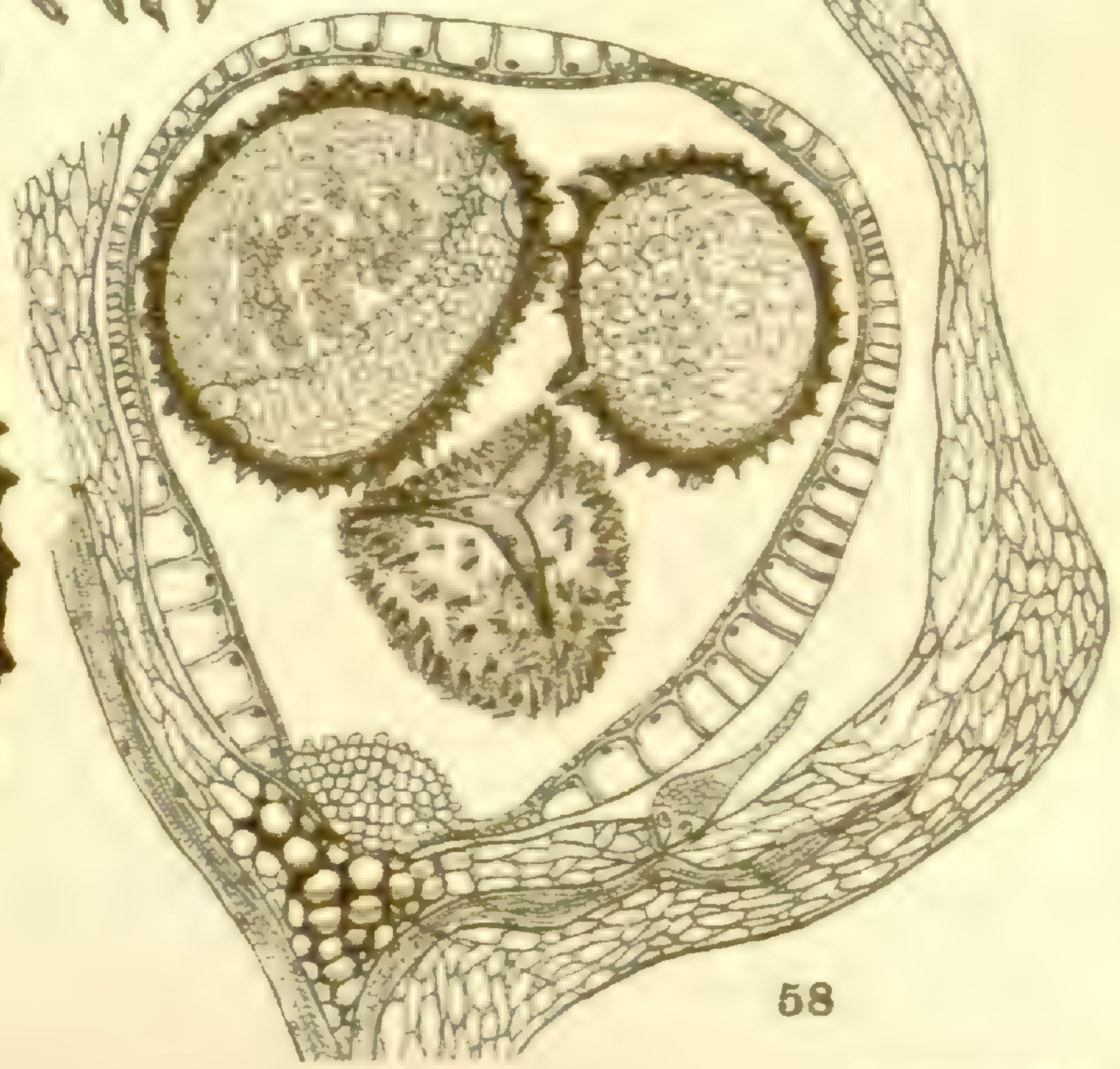
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megasporangia. Immediately upon the cessation of growth in the strobilus and during its ripening, a vegetative lateral bud on the axis immediately below the strobilus is stimulated into activity, develops horizontal branches, and roots which grow down into the humus. When this new growth is thus made independent, the axis bearing the strobilus and the germinating embryos decays, and at the period when cotyledons and roots of the young sporophytes are thrust out of the sporangia, the strobilus is lying in contact with the ground, shaded and otherwise protected by the vigorous vegetative growth that is spread above them. The strobilus decays much more slowly than the leafy axis beneath. This accounts for my finding strobili which appear to be shed from the plants. In case a strobilus fails to produce embryos, either through failure in fertilization, or probably more often because the dry season overtakes the gametophyte at a critical stage of its growth, the strobili continue to grow indeterminately throughout the season, and apparently perform the vegetative work that, under more auspicious conditions, is taken up by the new growth from the lateral bud. Moreover, the spores rendered sterile by adverse conditions are shed from the sporangia. Thus not infrequently one finds greatly elongated strobili with a basal zone of empty gaping sporangia, surmounted by two or three whorls of empty microsporangia, then a zone of sprouting embryos, and an apical region of degenerating young stages of megasporangia. In contrast with this are the strobili which have developed under continuous favorable conditions, in which the *basal zone* displays embryos. Whether or not the strobilus may carry on its growth a third year in case of two successive failures to produce embryos, remains to be demonstrated. It will be a matter of interest to discover what variation in ecological conditions causes the strobili of the allied Texas species to pass the winter in a microsporangiate condition, whereas *S. rupestris* in Massachusetts appears to bear during the same season only megasporangia.

The University of Chicago.

[*To be continued.*]

BRIEFER ARTICLES.

THE PROBABLE FUNCTION OF CALCIUM OXALATE CRYSTALS IN PLANTS.

A RATHER comprehensive study of vegetable histology (medicinal plants), extending over a period of six years, has brought to my attention more specifically the great abundance and wide distribution of crystals of calcium oxalate, and has led to the formulation of a theory as to their probable function in the plant economy.

There seems to be no logically deducible reason for assuming that the crystals serve as a protection against herbivorous animals, though such a theory was promulgated by Stahl and others and is now widely accepted by teachers of botany.

Calcium oxalate occurs in four predominating form types. Of these the least common is the crystal sand (Krystallsand, Krystallmehl, Krystallpulver) which occurs in the roots of belladonna, in the stem parenchyma of *Solanum dulcamara*, species of Atropa, Datura, Physalis; bark of Sambucus, Cinchona, and in some other plants. The prismatic and aggregate forms are perhaps about equally common and are very widely distributed. The needle-shaped or acicular crystals are also very common, but predominate in monocotyledonous plants.

Leaving out of consideration the still undecided question of the chemical formation of the crystals in the plant and the causes which lead to the production of one or the other form type, we shall refer briefly to their probable function.

G. Kraus in 1891 expressed it as his opinion that calcium oxalate was a reserve product to be redissolved by the plant and again utilized. This applies, however, only to a part of the crystals deposited during the previous season. Calcium oxalate dissolves with difficulty. It is insoluble in water, alcohol, ether, acetic acid, saliva, and other animal secretions. Being insoluble in these substances it is also tasteless; hence taste cannot enter as a factor to guard against destruction by herbivorous animals. Nor is this substance poisonous. Some of it would no doubt be decomposed by the secretions of the digestive tract (as free hydrochloric acid in the stomach), but not enough to produce poisoning due to the oxalic acid liberated. It is generally admitted that the oxalic acid in various plants, as Rheum, Rumex, etc., serves as a protection against animals, not because of its highly poisonous nature, but because of the extremely sour and astringent taste.

The theory that calcium oxalate serves to keep away animals through mechanical interference is highly improbable for several reasons. If this were the case the crystals would be peripherally located, as in this position they would soonest produce the desired effect. The crystals actually occur about uniformly distributed through the tissues of the various plant organs, and are in many instances especially abundant in the interior, as in the spongy tissue of leaves, the pith of stems, and the heart wood of stems. This mechanical interference can have application to small animals only, such as snails, insect larvae, etc. The crystals could not possibly injure or repel large animals capable of destroying the entire plant rapidly.

Based upon observation, the conclusion is reached that the prime function of calcium oxalate in plants is that of mechanical support; secondarily it plays the part of a reserve product as stated by Kraus. The following are the chief reasons in favor of the mechanical support theory:

1. Cells containing prismatic crystals are quite generally associated with bast fibers. These crystal-bearing fibers consist of rows of rectangular, thin-walled cells, each cell bearing, as a rule, a single crystal. The cells surround the bast fibers or bast bundles. They are very abundant and distinct in the bark of Salix, Quercus, and Populus, for example. They enclose completely the single enormous bast cells of quebracho, and occur in the majority of bast-bearing barks and stems, and are associated with the bast tissue of vascular bundles. Bast cells are essentially non-elastic; the crystal-bearing cells and fibers enclosing the bast give elasticity. This is shown to a remarkable degree in the inner bark of Quillaja, which contains an enormous quantity of large, elongated prismatic crystals of calcium oxalate distributed through the bark parenchyma.

2. In other instances the crystal-bearing cells are not merely an aid to mechanical tissues, but serve as a substitute therefor, functionally taking the place of sclerenchyma. For example, in the seed of quince there is found a sclerenchymatous tissue below the layer of mucilaginous epidermal cells. In the white garden bean this sclerenchymatous tissue is replaced by a layer of cells carrying large prismatic

crystals so constructed and placed as best to resist vertical and diagonal pressure, as of soil particles and the weight of the bean.

In the case of acicular crystals, so prevalent in monocotyls, it is evident that they give elasticity as well as support against crushing pressure. This applies especially to the very long and comparatively thick needles of calcium oxalate found in squill, iris, and other members of the lily family. These crystals (raphides) are especially common in the parenchyma of roots, rhizomes, tuberous roots, stems, and leaves.

It is generally admitted that the cystoliths of Ficus leaves, etc., perform a purely mechanical function. In plant organs subjected principally to a radial pressure, as are thick roots, tubers, thick rhizomes, etc., not specially supplied with mechanical elements, the aggregate crystals predominate, *e. g.*, Rheum and Rumex. In such organs as potatoes, corms of Colchicum, etc., the necessary mechanical support is given by the starch which fills the cells. A potato free from starch would be crushed by the soil in which it grows.

Further evidence in favor of the mechanical support theory of calcium oxalate is to be deduced from the fact that in many instances the crystals are imbedded in a gelatinous or mucilaginous substance which equalizes the pressure exerted, acting as a bumper between cell-wall and crystal. In other instances the cell-sap takes the place of the mucilage.

It is very frequently found that cells bearing calcium oxalate take the place of mechanical cells in leaves. The crystals are especially common in the cells bounding the air chamber of stomata which certainly require some mechanical support.

It is also highly probable that calcium oxalate is merely accidentally present in some plants and plant organs, but in the majority of instances its presence points toward a function of mechanical support as indicated.— ALBERT SCHNEIDER, *Northwestern University School of Pharmacy, Chicago.*

CURRENT LITERATURE.

BOOK REVIEWS.

Perception and propagation of stimuli in roots.

A NEW FIELD of research in plant tropisms has recently been opened by Němec in two important papers dealing with the normal and pathological cytology of the cells of sensitive and curving regions of roots and stems. In the first of these[1] the author shows that there exist starch grains in the cells of the root caps of many roots, and in several other sensitive regions. These grains invariably occupy the physically lower side of the cells in which the lie. Most of the experiments were conducted upon the roots of seedlings and upon the coleoptiles of grasses. At the close of an experiment the organs were killed, and studied by staining and sectioning. The movement of the grains occupies a comparatively short time, a half hour being sufficient for their rearrangement in the cells of the root cap in Pisum, when this has been turned on one side. The grains are embedded in the plasma, and as they fall away from that part of the protoplasm against which they normally lie (*i. e.*, when the organ is upright), the protoplasm on that side of the cell becomes altered so that it stains much more deeply. If the organ has been so placed that when the grains come to rest they still lie against a part of the normally lower wall, only that part of the protoplasm which has been freed from them becomes altered. Cells which have been in an upright position, but have lost their starch, owing to the influence of a plaster jacket, show the same proptoplasmic thickening as those which have been turned so that the grains fall by gravitation away from their normal position. Roots so treated are found to have lost their power of geotropic curvature. The author suggests that this may be due to the loss of the starch. Also, when these roots are freed from the plaster and allowed to renew their growth, they regain their normal sensitiveness. The return of sensitiveness is accompanied by the formation of new starch grains in the root cap. Also, if the region containing the grains be cut away, geotropic reaction ceases for a time, and its return is simultaneous with the formation of new grains in the regenerated tissue.

Němec is of the opinion that the stimulus for geotropic curvature is the change of pressure of the starch grains upon the protoplasm. These variations in pressure are of such small magnitude, however, that it is well-nigh inconceivable that they should produce an effect great enough to be propagated through many cells and produce a reaction. It seems much more probable to us that the sensitiveness is due rather to a chemical than to a physical change of condition within the cells. This seems the more probable on account of the fact that when the grains leave their normal position, the protoplasm here becomes changed. Possibly this may be due to the removal, not of the grain, but of the leucoplast in connection with it. The chemical effect of the leucoplast upon sugars passing through it is very great (since it produces in them condensation to form starch), and it may well be that it also has an effect upon the surrounding protoplasm. There may be other, as yet invisible, substances within the cell, which cannot diffuse readily, whose specific gravity differs from that of the protoplasm, and these might affect the protoplasm unsymmetrically, thus setting up a stimulus which could be propagated to the curving region.

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[1] NĚMEC, B.: Ueber die Wahrnehmung des Schwerkraftreizes bei den Pflanzen. Jahrb. f. wiss. Bot. **36**: 80–178. 1901.

The second paper[2] treats of the conduction of the stimulus from the sensitive regions to the region of the curvature. Traumatropic responses in roots were chosen as field for experimentation. If the tip of an Allium root is wounded by a cut or needle thrust, the protoplasm of the meristematic cells bordering upon the wound heaps up and becomes more dense on the side toward the wound. The nucleus also migrates toward the wound, often coming to lie against the wall on that side of the cell. After a very short time these cells regain their normal condition. But in the meantime a second and third layer of cells, at the side of and behind the wound, have responded in the same manner. Thus in roots killed 15 minutes after wounding, the response has been propagated through 1.25^{mm} of tissue, but those cells within 1^{mm} of the wound have already regained their original condition. This propagation takes place most rapidly in a longitudinal direction, but only towards the base of the root. It also occurs in both directions laterally.

A careful investigation was made to determine whether this difference in the rate of propagation of the response might correspond to any difference in structure. In the cells taking part in the traumatropic reaction, longitudinal strands of protoplasm can, by proper staining, be made visible with comparatively low magnification. Sometimes there is a single strand, sometimes several; sometimes they lie near the middle of the cell, and sometimes, especially in vacuolated cells, along the lateral walls. The strands are always in contact with the nucleus, often dividing and enclosing this body between several branches which reunite beyond it. A differential stain for the branches has not been discovered, but they take the ordinary stains much more deeply than the surrounding protoplasm. The best results were obtained by staining strongly with fuchsin S.

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[2] NĚMEC, B.: Die Reizleitung und die reizleitenden Strukturen bei den Pflanzen. 8vo. pp. iv + 154. *pls. 3. figs. 10.* Jena: Gustav Fischer. 1901. Cf. note BOT. GAZ. **31**: 133. 1901.

By use of high magnification the protoplasmic strands in Allium root tips can be shown to be bundles of fibrillae. These fibrillae have a definite sheath and lie embedded in a special plasma. In other plants the fibrillae could not be so well made out, but enough was accomplished to convince the author that, in general, the longitudinal strands are fascicles of smaller fibrils. In longitudinally adjacent cells the strands (and in Allium, at least the fibrillae also) correspond on the opposite side of cross walls, and the author supposes that the fibrillae are in contact, or perhaps continuous, through these walls. Transverse fibrils were found in certain cells, but never in bundles.

The question whether or not these fibrillae have any connection with the transmission of traumatropic and other stimuli is a difficult one to answer. The influence of a number of changes in external conditions was determined, first with regard to the propagation of the traumatropic reaction, and then with regard to the fibrils. It was found that the conditions which cause a degeneration of the fibrillae diminish the rate of propagation or cause this phenomenon to cease altogether. By a sudden change in temperature the fibrils may be caused to degenerate, but later (unless the change is too great) they form again. The same change lessens the rate of, or puts an end to, propagation of the traumatropic response in the longitudinal direction, but after a time the cells regain their power to respond normally. The return of this power to the cells is always accompanied by the regeneration of the fibrillae.

Another line of evidence is furnished by the study of certain roots of Allium which exhibited an apparently spontaneous nutation, uninfluenced by gravity. In these the starch-bearing cells of the root cap were perfectly normal in appearance and behavior, but in almost all of these roots the bundles of fibrillae were disorganized. Still other evidence was obtained from *Vicia faba.* In roots of this plant the fibrillae are found only in the large plerome cells. If the plerome is severed by a knife-thrust the geotropic reaction either occurs not at all, or bending takes place only so far up the root as the wound. Němec concludes that the bundles of fibrils are the path of conduction for traumatropic, geotropic, and other stimuli. The fibrils are strands of protoplasm specialized for conduction.

The two pieces of research here reviewed are accompanied by figures which are certainly convincing with regard to the facts. To us it appears that the conclusions of the second paper are much better supported by experiment than those of the first. The bundles surely bear a close relation to the process of conduction, whether this relation be causal or not. The author compares the fibrils to the nerve fibers of animals, but it seems to us that there is little similarity.—BURTON EDWARD LIVINGSTON.

Two new books on plant physiology.[3]

THE dearth of text-books on plant physiology seems about at an end. We record with pleasure the almost simultaneous publication of two books on this subject, one by Professor D. T. MacDougal, of the New York Botanical Garden, the other by Professor W. F. Ganong, of Smith College. It is significant that both these books are American.

The first named volume comprises a very comprehensive, though necessasarily brief, account of the phenomena of plant physiology, together with explicit directions for laboratory experimentation. Discussion of principles and laboratory directions are so interwoven that the temptation for the student to work mechanically, without other end in view than to finish the experiment, must here be reduced to a minimum. For this reason the book may be found more useful on the laboratory table than in the reading room. The mere reader will often be disappointed by the absence of measurements, etc., since it is intended that these shall be obtained in the laboratory. On the other hand, it will be well-nigh impossible for one to peruse any section without gaining a fair knowledge of the methods by which the principles there treated are established.

After an introductory chapter on the nature and relations of an organism (in which many statements are unavoidably made which the student cannot understand until he has gone further) the author devotes seven chapters to the presentation of the subject of irritability. In each of these a group of external conditions and the influence of these upon the plant is taken up. These chapters are headed as follows: Relations of plants to mechanical forces, Influence of chemicals upon plants, Relation of plants to water, Relation of plants to gravitation, Relation of plants to temperature, Relation of plants to electricity and other forms of energy (although there are no "other forms" mentioned here), and Relations of plants to light. The chapter on the influence of chemicals will be found especially valuable. The next chapter (IX) deals with the composition of the body, and consists of a very brief treatment of the different groups of compounds found in the plant, followed by methods for their extraction, separation, and identification. This discussion is so brief that the reader may be led into error by generalizations; and students will need to be cautioned that the qualifying phrases in the chapter are very important.

Following this are five chapters on the processes going on within the living plant. These are entitled: Exchange and movements of fluids, Nutritive metabolism, Respiration, Fermentation and digestion, Growth, and

[3] MACDOUGAL, D. T.: Practical text-book of plant physiology. 8vo. pp. xiv + 352. *figs. 159.* New York: Longmans, Green & Co., 1901.

GANONG, W. F.: A laboratory course in plant physiology, especially as a basis for ecology. 8vo. pp. vi + 147. *figs. 35.* New York: Henry Holt & Co., 1901.

Reproduction. The treatment of enzymes, which have become so important a consideration within the last few years, is comparatively full, both in the chapter on the composition of the plant and in that on nutrition, and will be especially useful.

Following the chapters on processes within the plant, the last chapter in the book gives a very excellent exposition of the subject of vegetative propagation throughout the plant kingdom. Sexual reproduction is not treated. At the end is a valuable appendix containing tables of physical constants, such as the expansion of air at different temperatures from 0° to 35°, the density of oxygen and of carbon dioxid, the absorption of these gases by water, etc. It will be a great aid, in experiments where calculation is necessary, to have these tables in a convenient form for reference.

Regarding the style, we wish it might have been clearer in places; there will surely arise difficulties of interpretation now and then. The only important point of theory wherein the author may find others in disagreement with him is that which expresses itself here and there in the idea of some *purpose* underlying the whole field of plant phenomena. For instance, it is stated that there exist "reactions to shock . . . . which the most thorough investigation has failed to invest with a purpose. New relations of the plant may be discovered, however, which will interpret these reactions."

The book is fully illustrated throughout, including many figures of apparatus. References to the most important recent publications on the different topics are given as footnotes, and both treatment and references are surprisingly up to date, articles being cited which appeared only a few months ago. The index is complete, and includes footnotes as well as text. The arrangement of the subject-matter is thoroughly scientific, which fact, together with its general completeness and reliability, should give the book a broad and constant use in laboratories where the subject is taught.

Professor Ganong's new book does not attempt to present any general discussion of the subject, but is designed, as its title denotes, for laboratory use only. It is divided into two parts, the first being on methods of study and necessary equipment, while the second comprises the true outline of the course. Part I is written largely for the teacher, and every teacher of laboratory science (whether it be physiology or not) will do well to read it. The first two sections of this part are especially noteworthy for their fund of pedagogical ideas, which, it seems to us, are almost all philosophically and practically sound. The third and fourth sections deal with laboratory, greenhouse, and materials for the course. Section 5 gives practical directions for a great number of laboratory manipulations, some of which often are a source of considerable trouble to the inexperienced. This will surely prove a very valuable part of the book.

Part II, the outline of the course itself, consists of two divisions. Division

I treats of the structure and properties of protoplasm, including its composition, its relation to external conditions, and its power of organism building. Division II deals with the physiological operations of plants. Here are included nutrition, growth, reproduction, irritability, locomotion, and protection. The last two are not treated, however, the statement being made that they are almost purely ecological in their nature.

The titles of the exercises throughout this entire part are put in the form of questions. The directions which follow are designed to aid the student in answering the question, but do not answer it for him. Just enough discussion is brought in with the laboratory directions to arouse the student's interest in the experiment in hand, and to make him appreciate what are its essential points. Ample references to the literature are constantly given, even to original articles; the author believes that direct contact with the sources of information is of great pedagogical value. Good half-tone reproductions of photographs show the student just how the more complicated forms of apparatus are to be set up. With their aid he should be able to bring his experiment to completion with a minimum amount of aid from the teacher.

Following this part are several pages of addenda in which are noted numerous improvements upon apparatus described in the body of the book.

The course as outlined by Professor Ganong will doubtless occupy more time than many can give to an elementary course in plant physiology. For such teachers the book will still be useful, since it is so well arranged that one can easily strike out a topic here and there without materially affecting the course as a whole. The style is clear, vivid, and scholarly throughout. We can think of no book yet published which might better "serve as a guide to the acquisition of a general physiological education."— BURTON EDWARD LIVINGSTON.

MINOR NOTICES.

THE *Transactions* of the American Microscopical Society **21**: 1900, contains 275 pages devoted largely to zoological papers and matters of general interest. The following are of special interest to botanists: C. A. KOFOID, *The plankton of Echo river, Mammoth cave;* HENRY B. WARD, *Comparative study of methods in plankton measurements;* GEORGE C. WHIPPLE, *Chlamydomonas and its effect on water supplies;* CHARLES E. BESSEY, *The modern conception of the structure and classification of diatoms,* with a division of the tribes and a rearrangement of the North American genera. Professor Bessey accepts Müller's view that the filamentous condition is the primitive one, and that diatoms should be regarded as typically filamentous rather than as unicellular forms. They should then be classed between the Peridiniales on the one hand, and the Desmidiaceae and Zygnemaceae on the other. The Zygnemaceae are regarded as the most primitive of the Conjugatae, while the desmids and diatoms are believed to represent two similar and somewhat parallel genetic lines in which the filaments tend to break up rather early into independent cells. The larger part of the paper is occupied by a key to the tribes and genera of the American forms.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS

EXPERIMENTS by D. Neljubow[4] have shown that the peculiar horizontal nutation of stems of seedling peas (*Pisum sativum*) grown in darkness at high temperature is due to the presence of small amounts of illuminating gas in the air of the laboratory. It is especially the acetylene and ethylene components of illuminating gas which are active. SO_2, and vapors of CS_2, xylol, and benzol are very injurious. This peculiar reaction to gas seems to have been unknown before.— C. R. B.

A FEW interesting points regarding the behavior of apples in cold storage are brought out in a bulletin[5] by L. C. Corbett on this subject. With the exception of York Imperial, the apples of all varieties tested lost less in weight when stored in the light than when kept in darkness. The acid content of the apples was markedly decreased during storage, while the sugar content was decreased in some varieties and increased in others. No explanation for these differences of behavior is attempted.— ERNST A. BESSEY.

A NUMBER of experiments throwing light on the method of infection in pear blight are described in a bulletin[6] from the Delaware Experiment Station. The germs were introduced by means of needle punctures into terminal shoots, one year old wood, three year old wood, buds, leaves, and fruit. Leaves and young twigs were smeared with cultures of the germ and kept moist for a time. The latter, however did not cause the disease to develop, for it appeared only where the germs had actually been introduced into the tissue, as for example, where needle punctures had been made into the present year's terminal shoots, into buds, leaves, and into the fruit. The punctures into three-year old wood produced only small diseased areas. The author's conclusions are that pear blight is only communicated, as pointed out by Waite, by transference of the germs by honey-seeking insects from nectary to nectary, and into the fruits, young succulent shoots, and leaves by the introduction through bites and punctures of insects of germs clinging to their mouth parts. The same bulletin reports the occurrence in Delaware of pear canker, which seems to be caused by *Sphaeropsis malorum*.

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[4] Beihefte z. Bot. Cent. **10**: 128–138. *figs. 2.* 1901.

[5] CORBETT, L. C.: Cold storage. Bull. West Virginia Agr. Expt. Sta. 74: 51–80. *figs. 1–3.* March 1901. Morgantown.

[6] CHESTER, F. D.: Pear blight and pear canker. Bull. Delaware Agr. Expt. Sta. 52: 1–8. *figs. 1–7.* April 1901. Newark.

Spraying with Bordeaux mixture is recommended as a preventive measure for this disease.— Ernst A. Bessey.

Dr. Bradley M. Davis has recently published[7] some interesting studies on the nucleus of Pellia. These studies were undertaken with the object of extending our knowledge of the cytology of the Hepaticae, and with the hope of throwing some light on the relationships of the various morphological manifestations of kinoplasm. To accomplish this three phases in the life history of the plant were examined, namely sporogenesis, the germination of the spore, and the vegetative activities in the seta. In the spore mother cell the spindles are organized in the same manner as that characteristic of the pteridophytes and spermatophytes. In the stages of spore germination asters with centrospheres were found during the prophase. These appear to be transitory structures, however, as they disappear before the daughter nuclei are formed. In the vegetative cells the spindles are formed in essentially the same fashion as that described by Hof and Němec for the vegetative cells of many spermatophytes. The kinoplasm here forms two caps fitting closely over the ends of the nucleus which has become elongated, and these caps are changed into the poles of the spindle. The writer concludes, however, that the kinoplasmic fibrillae, the centrospheres, and kinoplasmic caps are all secondary developments from the primal granular protoplasm which is the only form of kinoplasm in any sense permanent in the cell. The paper forms an extremely interesting contribution and contains much that is of importance on the cytology of the Hepaticae.—A. A. Lawson.

Centrosomes in flowering plants are described by Bernard[8] in a series of short papers. From a study of *Lilium candidum*, *L. Martagon* and *Helosis Guayanensis* the writer convinced himself of the presence of the much discussed structures. Material was fixed in alcohol and in Flemming's solution and was stained in a mixture of fuchsin and iodine green (1 per cent. aqueous solution of fuchsin, 2 parts; 1 per cent. aqueous solution of iodin green, 2 parts and water 40 parts). The safranin gentian-violet orange combination did not give as good results.

In *L. candidum* the centrosomes were found quite regularly during various phases in the germination of the megaspore. They resemble the structures described by Guignard, but are not so sharply defined. The centrosome was also identified in the gametophytes of Helosis. In *L. Martagon* centrosomes were found in the female gametophyte, in the vegetative cells of the ovule, but could not be positively identified in the endosperm. The centrosome is cytoplasmic in origin.

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[7] Nuclear studies on Pellia. Ann. Bot. **15**: 147–180. *pls. 10–11.* 1901.

[8] Bernard, C. H.: Recherches sur les sphères attractives chez *Lilium candidum*, *Helosis Guayanensis*, etc. Jour. de Botanique **14**: 118–124, 177–188, 206–212. *pls. 4–5.* 1900.

Incidentally, it is noted that there are sometimes two embryo sacs in *L. candidum*. In these species a very large vacuole develops between the two polar nuclei preventing the nuclei from fusing. The writer suggests that this may account for the sterility of this species. It is also noted that the upper polar nucleus and the nuclei of the egg and synergids are erythrophilous, while the four nuclei at the antipodal end of the sac are cyanophilous. This difference in chromatophily is attributed to chemical differences due to sexuality, the nuclei at the antipodal end of the sac having lost all sexual character.— Charles J. Chamberlain.

Items of taxonomic interest are as follows: H. J. Banker (Bull. Torr. Bot. Club **28**: 199–222. 1901) has published a synopsis of the species of Hydnum, 40 being recognized, and one described as new.—Aven Nelson (*idem* 223–235), in his 13th paper entitled "New plants from Wyoming," has described 18 new species and varieties belonging to various families.—David Griffiths (*idem* 236–241) has described a new ergot growing on species of Hilaria in Arizona.— Maxwell T. Masters (Bot. Jahrb. Beibl. **29**: no. 66. pts. 3–4. 1–20. D1900) has published numerous new species of Restionaceae from the Cape of Good Hope, including a new genus (*Phyllocomos*).— H. Christ (Bull. Herb. Boiss. II. **1**: 445–460. 1901) has published a number of new species of ferns from Dutch New Guinea.— In Torreya (**1**: 41–43. 1901) N. L. Britton has described a new Hieracium from Florida, E. L. Greene a new Arnica from Oregon, and W. J. Beal a new Panicularia from Colorado.— B. Shimek (Bull. Lab. Nat. Hist. Iowa Univ. **5**: 139–170. 1901) has published a list of the pteridophytes of Iowa, with stations.—T. Makino and K. Shibata (Bot. Mag. Tokyo **15**: 1-14. *pl. 1.* 1901) have described a new genus (*Sasa*) of Bambuseae, including eight species which have heretofore been referred to Bambusa. The name is a common Japanese name for "small bamboos."—Among some recently published notes on algae (Zoe **5**: 121–129. 1901) W. A. Setchell has described new genera as follows: *Hedophyllum* and *Pleurophycus* (both Laminariaceae), and *Weeksia* (Dumontiaceae).— B. L. Robinson (Proc. Am. Acad. **36**: 455–488. 1901), in a recent Contribution from the Gray Herbarium, has published as follows: A synopsis of the genus Melampodium, 36 species being recognized, 7 of which are new; a synopsis of the genus Nocca (Lagascea), 14 species being recognized, 3 of which are new; new species and newly noted synonymy among the spermatophytes of Mexico and Central America, the genus Eupatorium receiving 15 new species.— M. L. Fernald (*idem* 491–506) has described a fascicle of new seed-plants from Mexico and Central America. Among them is a new genus of Euphorbiaceae (Hippomaneae), *Alcoceria* by name.— William Trelease (Rept. Mo. Bot. Gard. **12**: 79–80. *pls. 35–37.* 1901) has published a new palmetto (*Sabal Uresana*) from Sonora.— J. M. C.

NEWS.

PROFESSOR MAXIME CORNU, of the Jardin des Plantes, Paris, died on April 3, in the fifty-ninth year of his age.

DR. DUNCAN S. JOHNSON, associate in botany at Johns Hopkins University, has been promoted to an associate professorship.

DR. ALEXANDER P. ANDERSON has been appointed assistant in botany in Columbia University to succeed Dr. M. A. Howe. Dr. Anderson will also carry on physiological studies at the New York Botanical Garden.

MR. GEORGE P. CLINTON, of the botanical department of the University of Illinois, spent last year at Harvard University on leave of absence. His leave has been extended for another year. He is at work upon the Ustilagineae.

DR. MARSHALL A. HOWE has been appointed assistant in the New York Botanical Garden and will devote himself especially to the study of the red algae. He is spending the summer in the eastern provinces of Nova Scotia, Cape Breton, and Newfoundland.

FROM *Science* we learn that Dr. H. W. Harkness, well known as a botanist of the Pacific coast, and especially for his recent studies on the Tuberaceae, died in San Francisco on May 10. His collections become the property of the California Academy of Sciences.

DR. F. L. STEVENS, who has spent the past year in Europe as an honorary fellow of the University of Chicago, has been appointed instructor in biology at the College of Agriculture and Mechanic Arts, Raleigh, North Carolina. He will have entire charge of the newly-established department.

DR. L. M. UNDERWOOD spent the months of June and July in botanical exploration in Porto Rico in connection with a party from the Department of Agriculture at Washington, consisting of O. F. Cook, special agent for tropical agriculture, Guy N. Collins, plant photographer, and Robert F. Griggs, botanical collector.

MR. H. HASSELBRING, a graduate of Cornell University and later assistant in botany at the New York Agricultural Experiment Station, Geneva, has been appointed assistant in botany in the Agricultural Experiment Station of the University of Illinois. Mr. Hasselbring will devote his attention chiefly to plant pathology.

CHARLES F. HOTTES, Ph.D., formerly an assistant in the botanical laboratory of the University of Illinois, has just returned from three years study at the University of Bonn. He is now promoted to an instructorship in botany, and is given charge of vegetable physiology. While abroad he gave chief attention to plant physiology and cytology. Some researches will be published shortly.

THE OPENING of the Minnesota Seaside Station at Point Renfrew, Vancouver island, took place June 21. Thirty students are in attendance. Evening lectures have been given by Miss Eloise Butler, of Minneapolis, Mr. K. Yendo, of the University of Tokio, Professor Conway MacMillan and Mr. Harold Lyon, of the University of Minnesota, and Professor Francis Ramaley, of the University of Colorado. The shore is exceedingly rich both in fauna and flora, and large collections are being made by some members of the party.

IN THE department of botany of the University of California Dr. W. J. V. Osterhout has been promoted to an assistant professorship. Professor W. L. Jepson is this summer exploring the western portion of the Colorado desert about San Jacinto mountain, in company with Mr. H. M. Hall, assistant in the herbarium. They will also make an exploration in Humboldt and Del Norte counties. Mr. N. L. Gardner, assistant, is making further studies of the algae of the Puget sound region. Dr. W. A. Setchell is at Pacific Grove, California, investigating the ecology and zonal distribution of the marine algae.

BOTANISTS will be interested in the organization of the new Bureau of Plant Industry of United States Department of Agriculture. The old divisional lines have been eliminated and instead the work has been divided into various related groups, as follows: Vegetable pathological and physiological investigations; Botanical investigations and experiments: Pomological investigations; Grass and forage plant investigations; Experimental gardens and grounds; Arlington experimental farm; Congressional seed distribution; Seed and plant introduction; and Tea culture experiments. The executive officers of the bureau are:

Beverly T. Galloway, physiologist and pathologist, and chief of bureau.

Albert F. Woods, pathologist and physiologist in charge of vegetable pathological and physiological investigations, and acting chief of the bureau in the absence of the chief.

Frederick V. Coville, botanist, in charge of botanical investigations and experiments.

F. Lamson-Scribner, agrostologist, in charge of grass and forage plant investigations.

Gustavus B. Brackett, pomologist, in charge of pomological investigations.

The pathological investigations are conducted by the following staff: Erwin F. Smith, pathologist, in charge of laboratory of plant pathology; Walter T. Swingle, physiologist, in charge of laboratory of plant physiology;

Herbert J. Webber, physiologist, in charge of laboratory of plant breeding; Newton B. Pierce, pathologist, in charge of Pacific coast laboratory; Hermann von Schrenk, special agent, in charge of Mississippi valley laboratory; Peter H. Rolfs, pathologist, in charge of tropical laboratory; Merton B. Waite, assistant pathologist, diseases of orchard fruits; Mark Alfred Carleton, cerealist; C. O. Townsend, pathologist; George T. Moore, physiologist; B. M. Duggar, physiologist; Rodney H. True, physiologist; William A. Orton, assistant pathologist; Joseph H. Chamberlain, expert in physiological chemistry; Thomas H. Kearney, assistant physiologist; Cornelius F. Shear, assistant pathologist; Flora W. Patterson, mycologist.

The botanical investigations and experiments are conducted by the following staff: O. F. Cook, botanist, in charge of tropical agriculture; A. J. Pieters, botanist, in charge of seed testing laboratory; V. K. Chestnut, botanist, in charge of investigations of poisonous weeds; Lyster F. Dewey, assistant botanist; Carl S. Schofield, expert on cereals.

The following have charge of the grass and forage plant investigations: A. S. Hitchcock, assistant agrostologist, in charge of field work; David Griffiths, assistant agrostologist, in charge of field management; Elmer D. Merrill, assistant agrostologist, in charge of collections; C. R. Ball, assistant agrostologist.

The officers of the pomological investigations are: William A. Taylor, pomologist, in charge of field investigations; H. P. Gould, pomologist, in charge of fruit district investigations; George C. Husmann, expert, in charge of grape investigations.

The following branches are conducted under the direction of the chief of the bureau, but the officers directly in charge are given under each branch:

Experimental Gardens and Grounds: L. C. Corbett, hoticulturist; E. M. Byrnes, head gardener; George W. Oliver, expert plant propagator.

Congressional Seed Distribution: Robert J. Whittleton, superintendent of weighing and mailing section; James Morrison, superintendent of records.

Seed and Plant Introduction: Ernst A. Bessey, assistant in charge; David G. Fairchild, permanent agricultural explorer.

Arlington Experimental Farm: L. C. Corbett, horticulturist, in charge.

Tea Culture Experiments: Dr. Charles U. Shepard, in charge.

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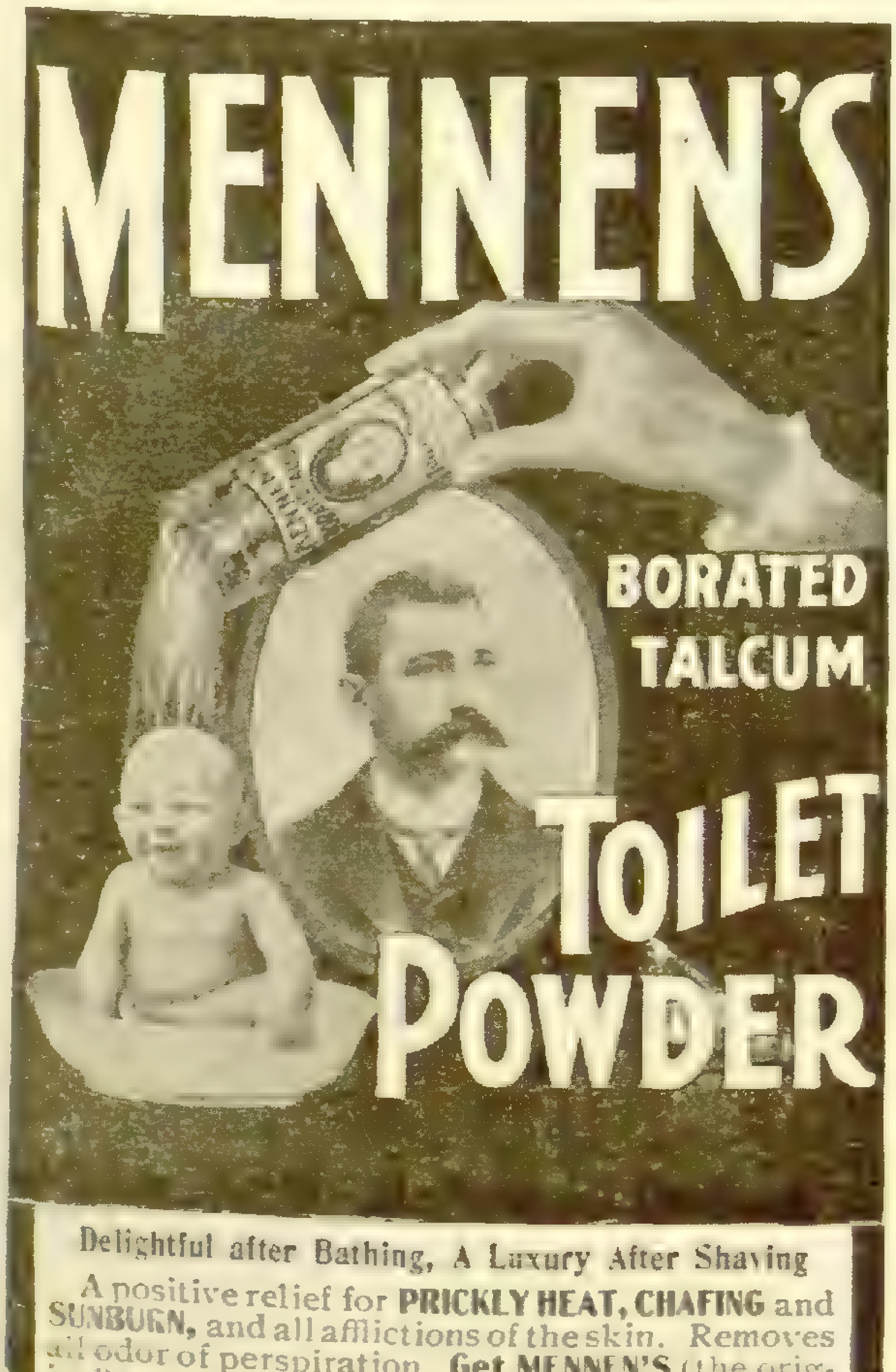

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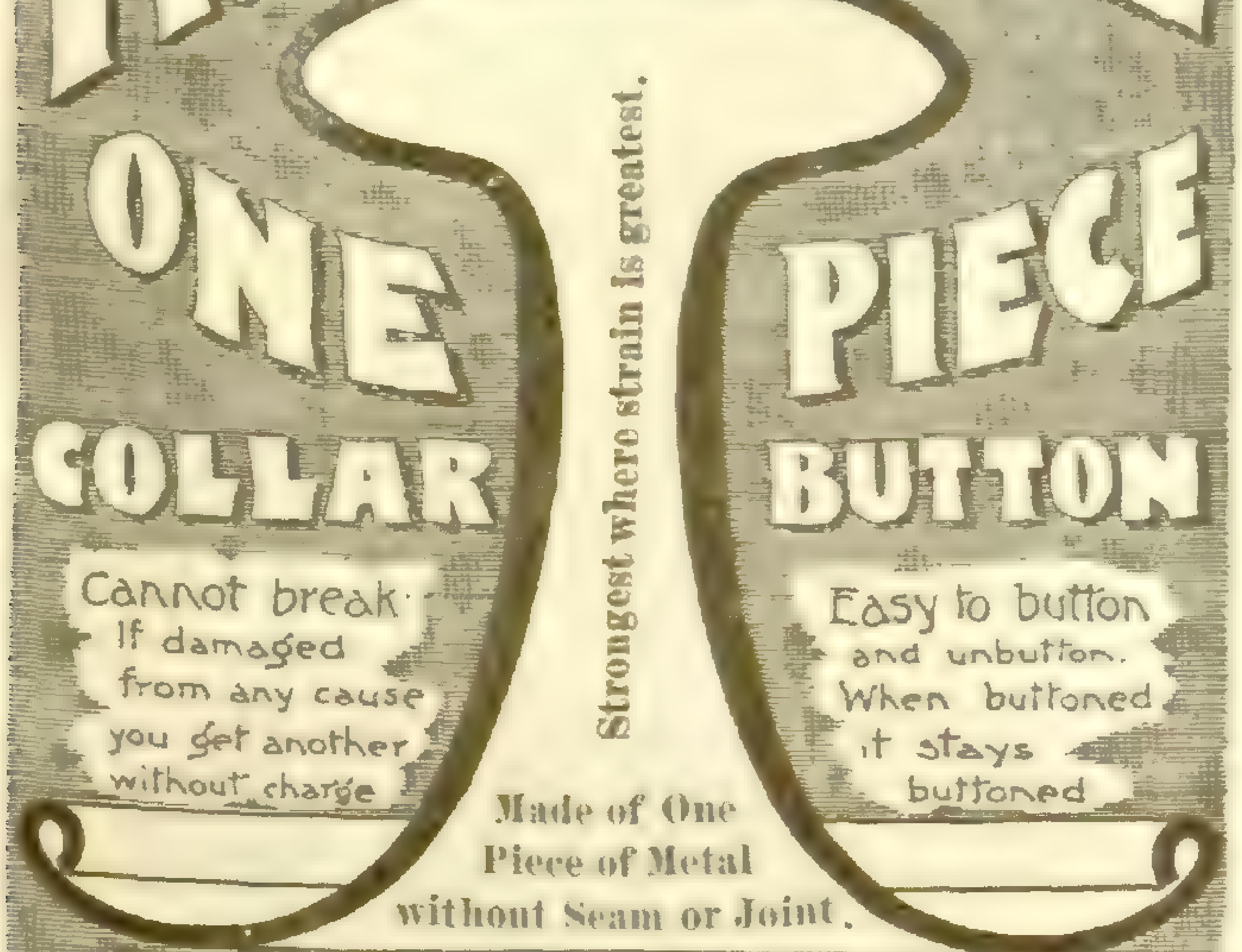

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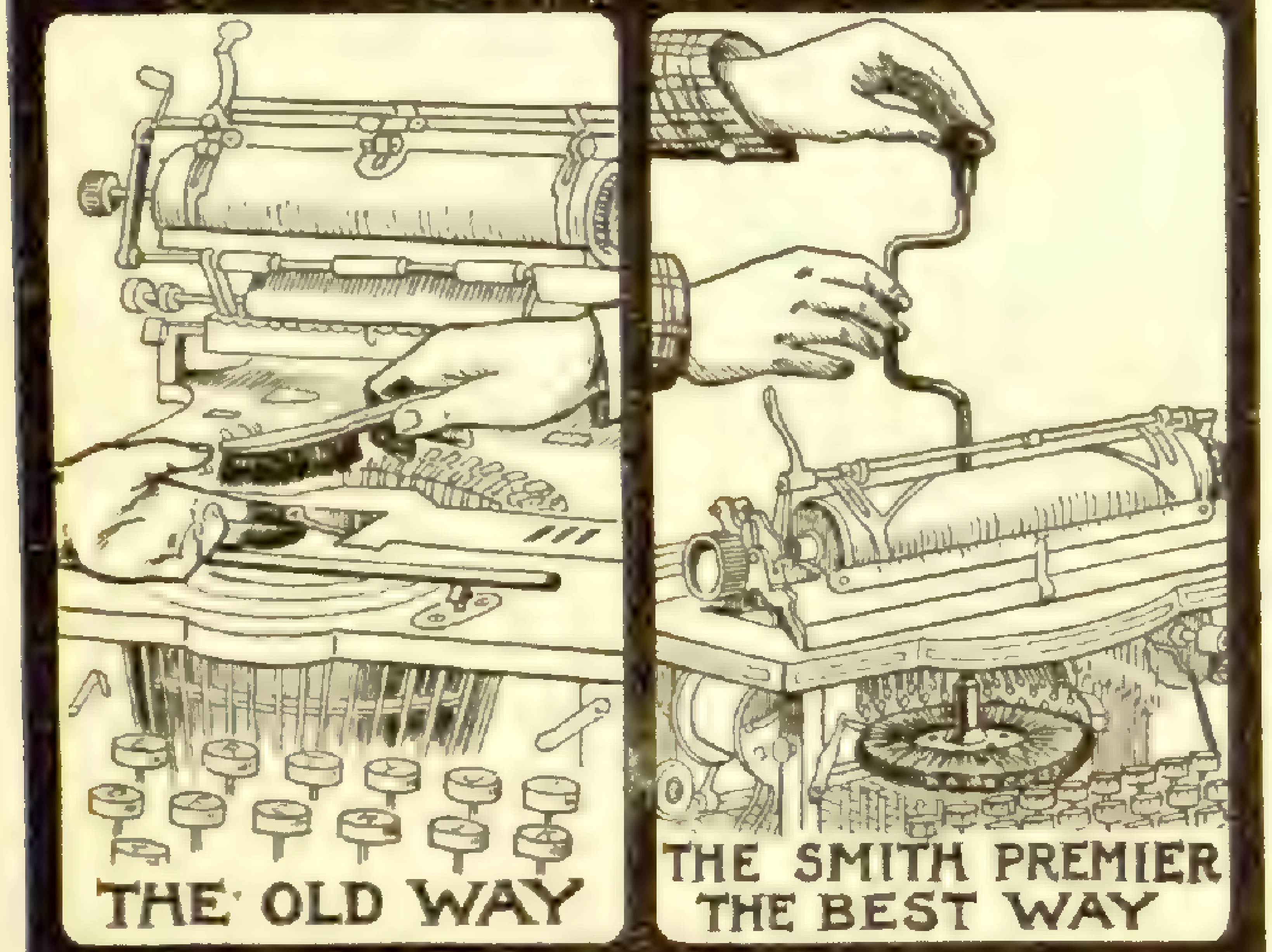

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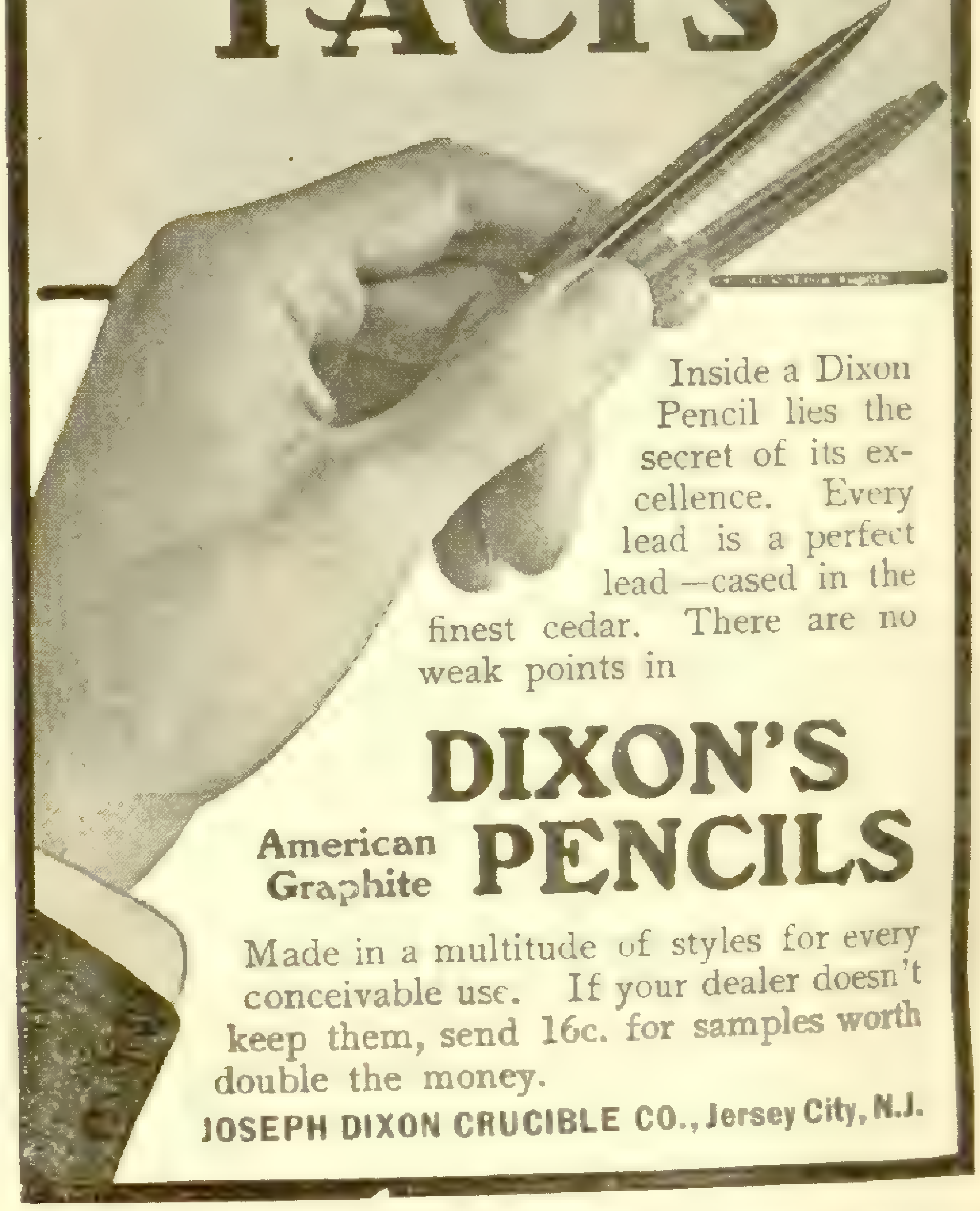

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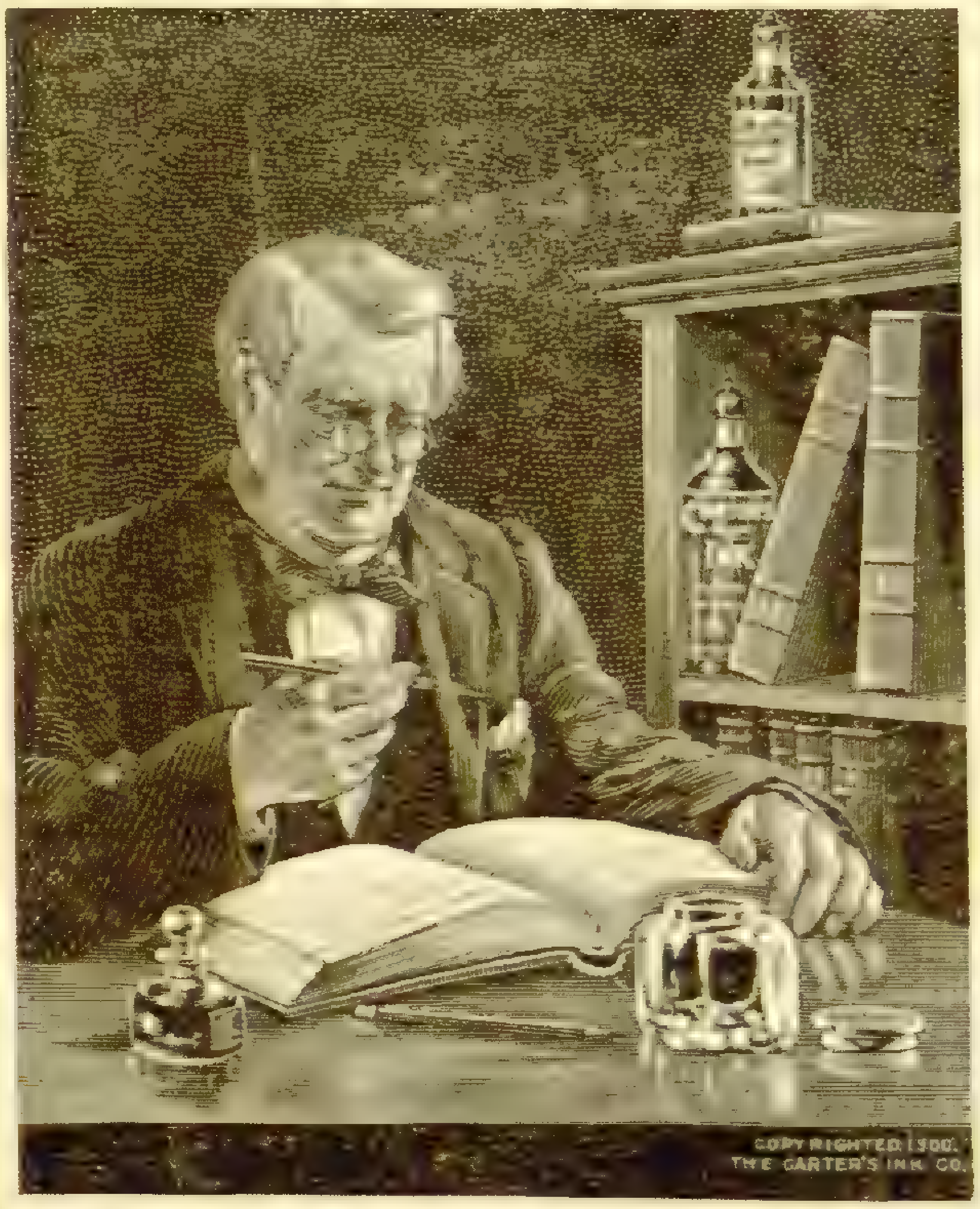
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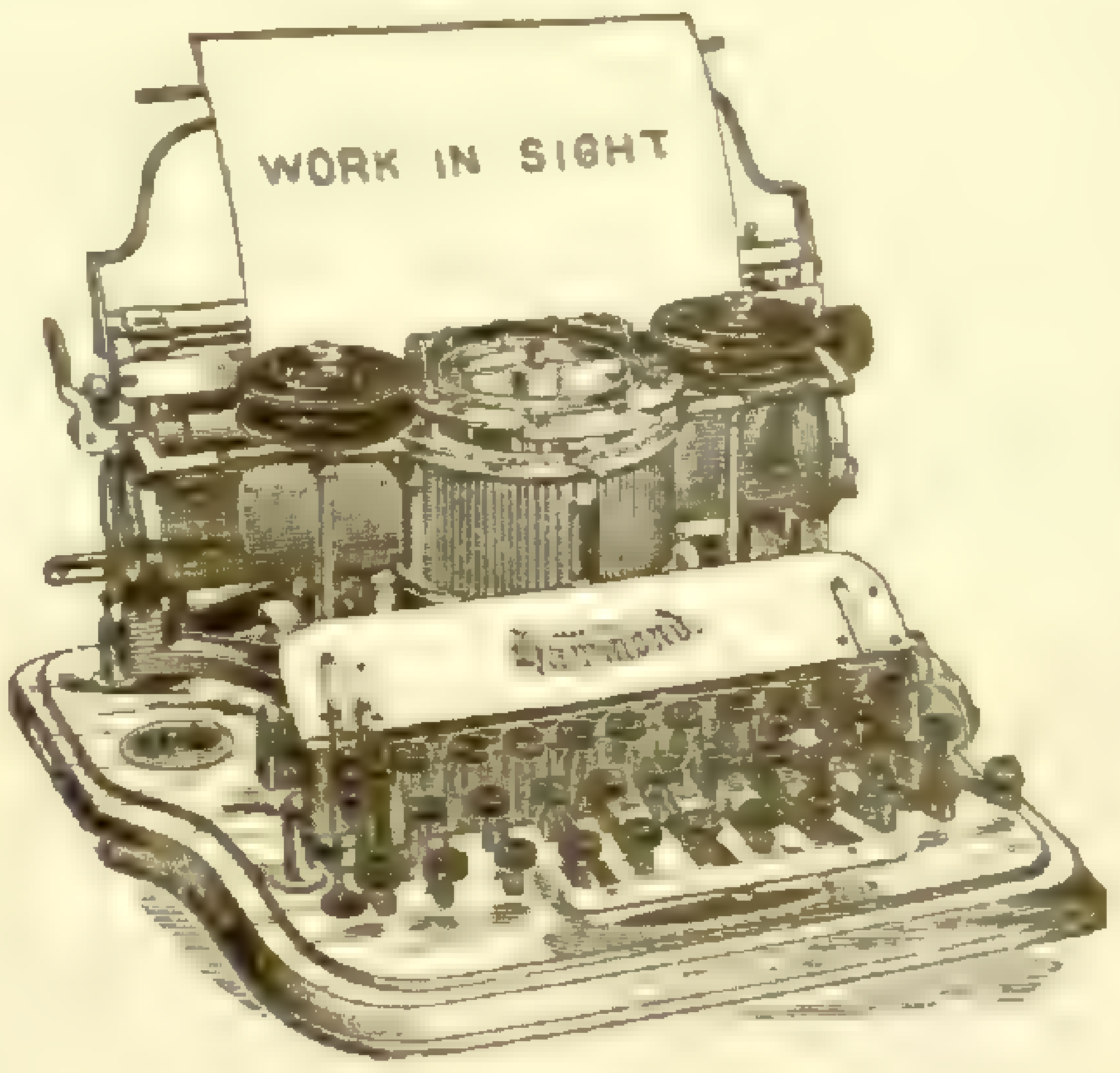

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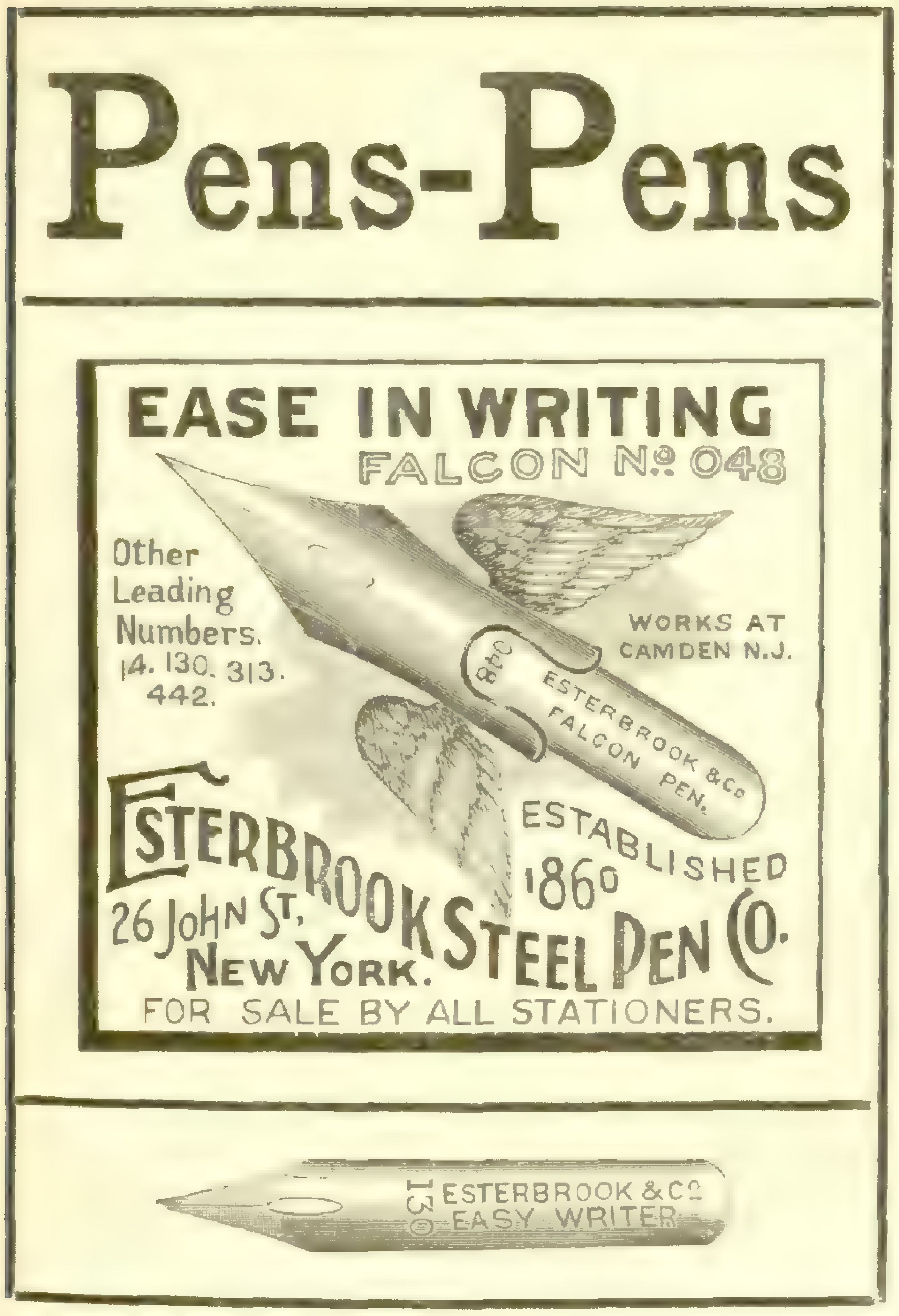

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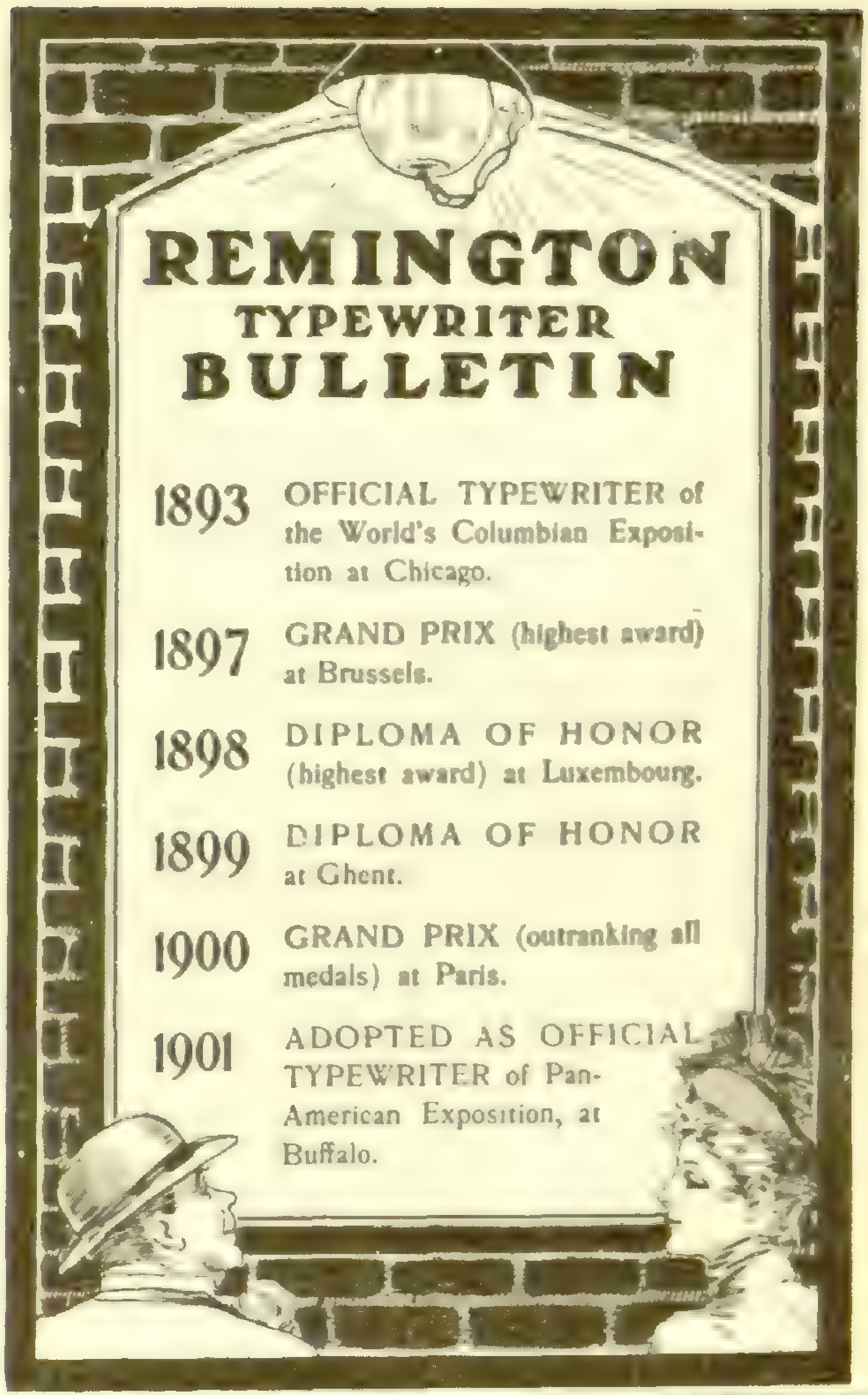

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Moses C. White.
S. H. GAGE, Cornell University, ... 1109
Fire in the Veterinary College at Cornell.
S. H. GAGE, ... 1111
Laboratory Photography.
Stereo Photo-Micrography, ... 1113
The New York Botanical Garden.
D. T. MAC DOUGAL, ... 1115
Preliminary Study of Mycetozoa.
CLARA LANGENBECK, Wells College, ... 1119
Micro-Chemical Analysis, X. Potassium.
E. M. CHAMOT, Cornell University, ... 1121
Easy Method of Mounting and Preserving Mosquitoes.
V. A. LATHAM, M. D., ... 1129
Current Botanical Literature.
CHAS. J. CHAMBERLAIN, University of Chicago, ... 1131
Cytology, Embryology and Microscopical Methods.
AGNES M. CLAYPOLE, Cornell University, ... 1133
Normal and Pathological Histology.
RICHARD M. PEARCE, M. D., Harvard College, ... 1136
General Physiology.
RAYMOND PEARL, University of Michigan, ... 1138
Current Bacteriological Literature.
H. W. CONN, Wesleyan University, ... 1141
Notes on Recent Mineralogical Literature.
ALFRED J. MOSES, LEA McI. LUQUER, ... 1144
Medical Notes, ... 1145
News and Notes, ... 1147

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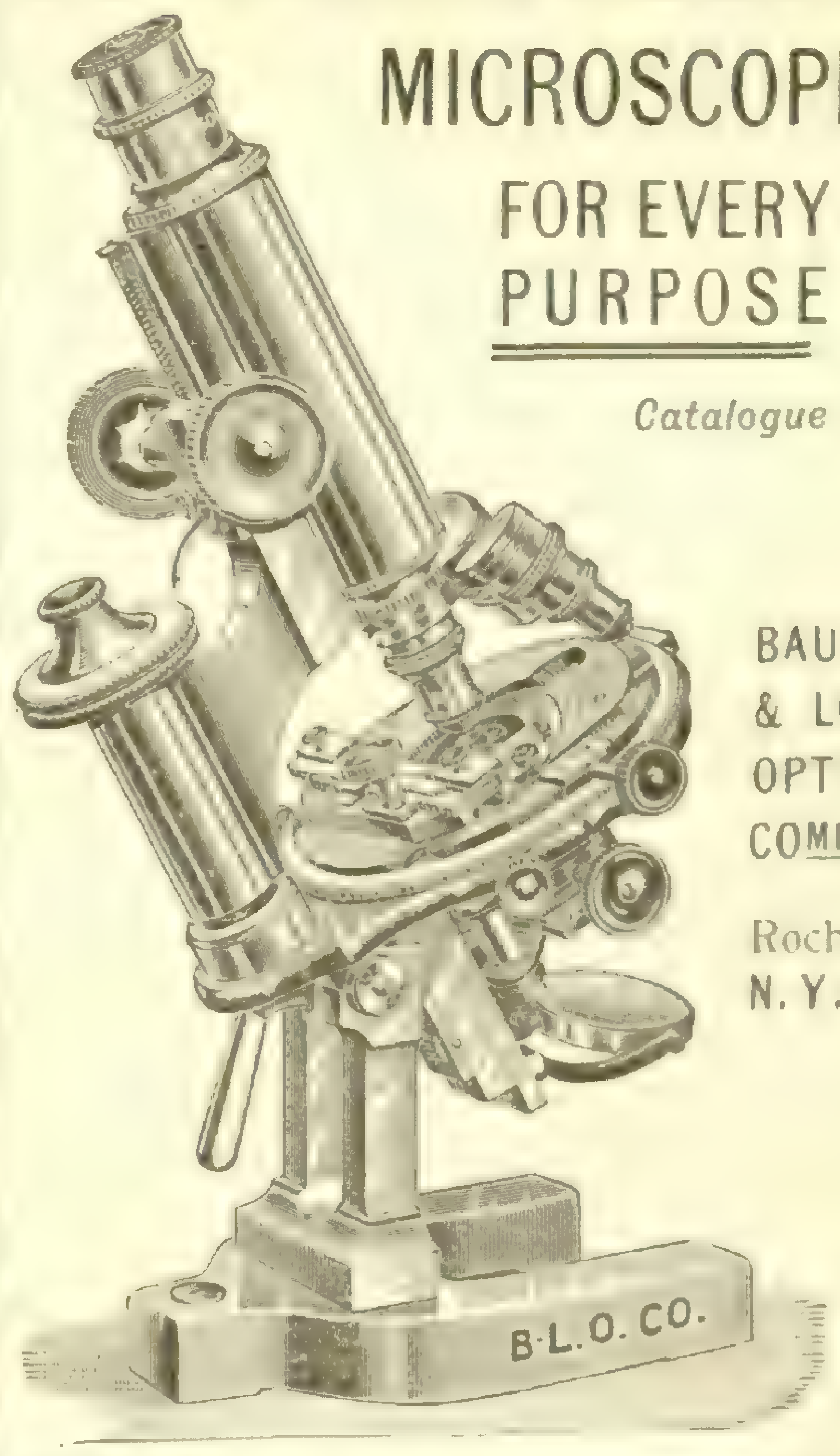

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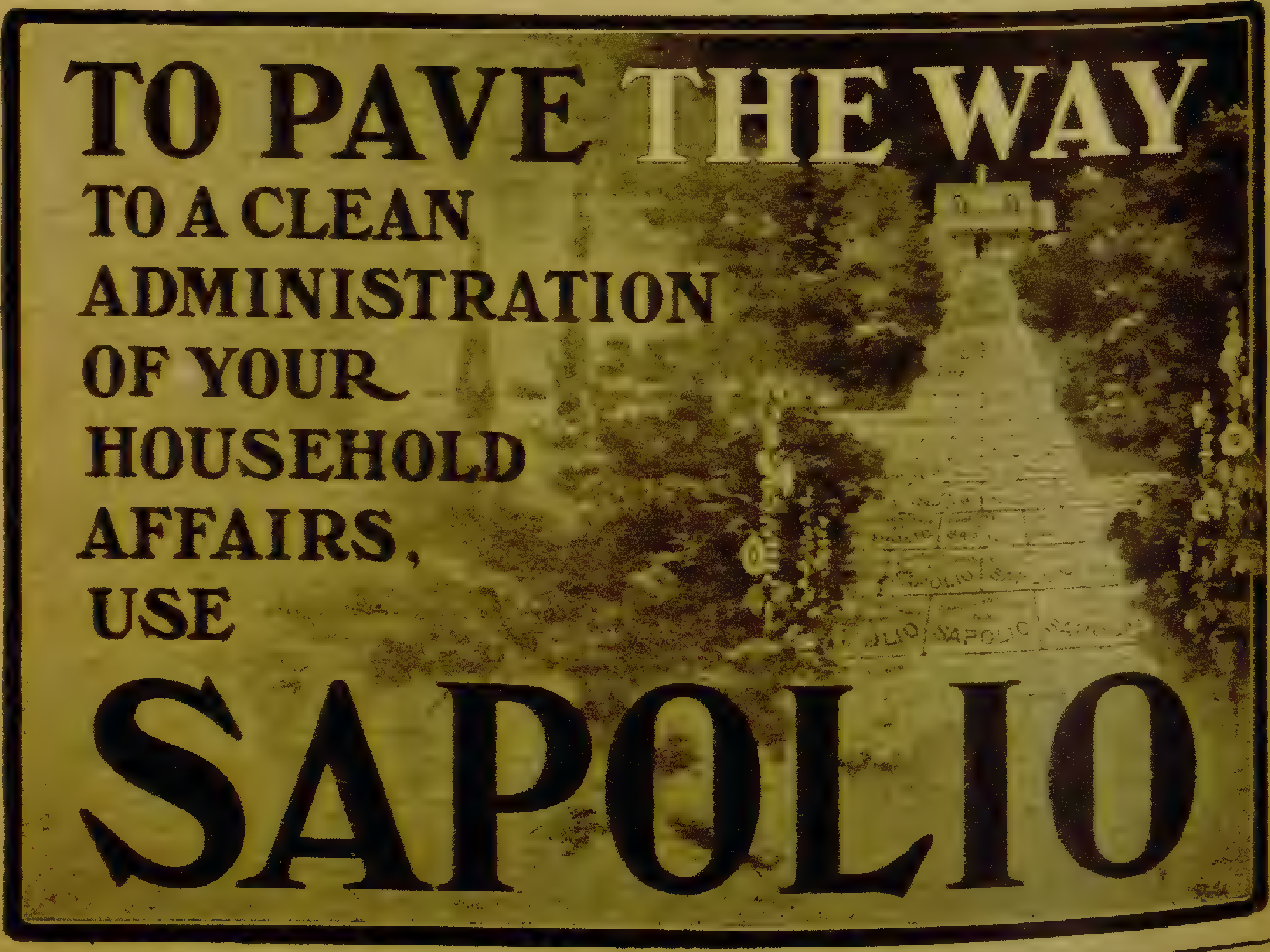
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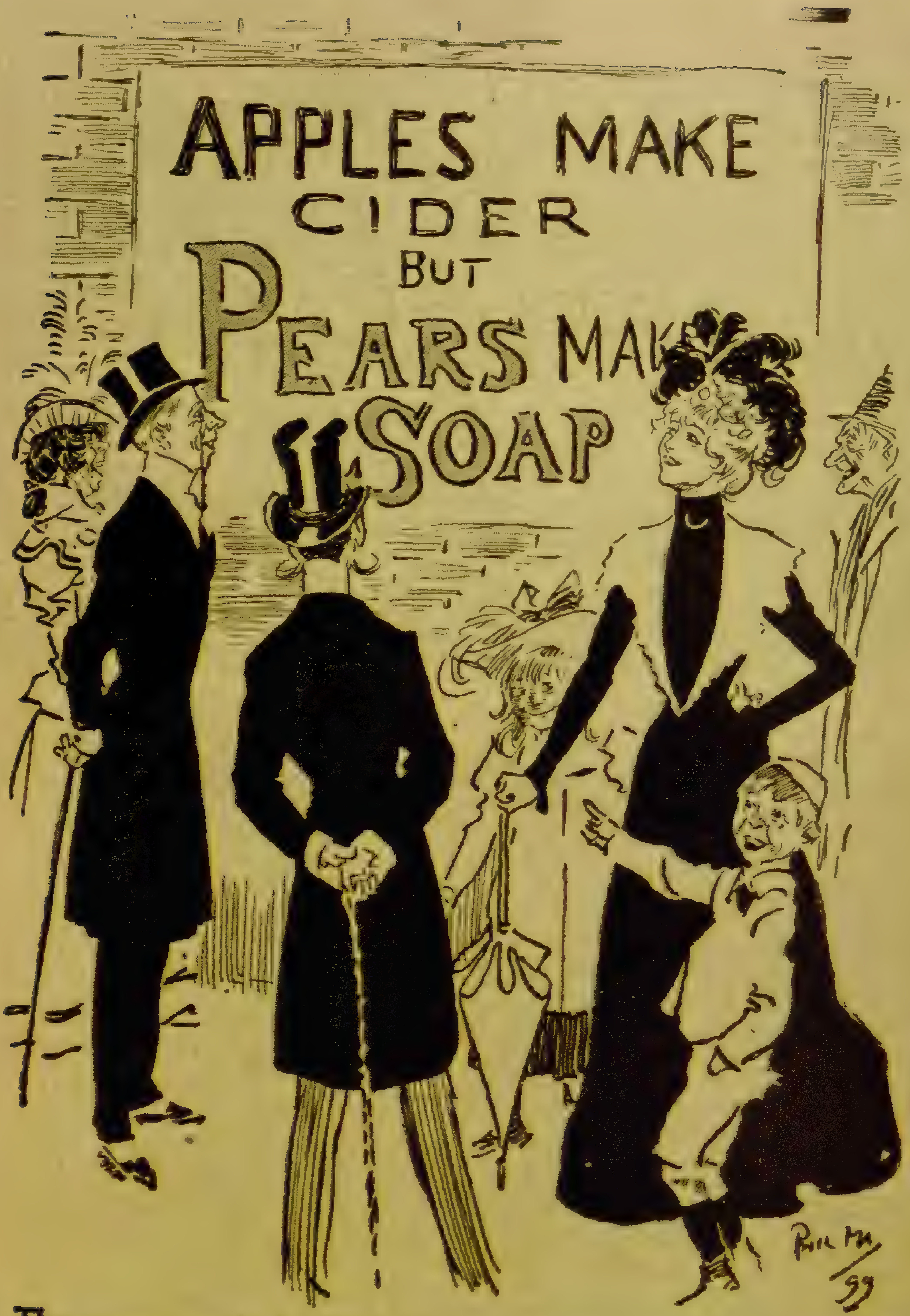
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CONTENTS

GAMETOGENESIS AND FERTILIZATION IN ALBUGO. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX. (WITH PLATES I–IV.) *Frank Lincoln Stevens* - 157

A STUDY OF THE SPORANGIA AND GAMETOPHYTES OF SELAGINELLA APUS AND SELAGINELLA RUPESTRIS. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXI. (WITH PLATES V–IX.) *Florence May Lyon* - - - - 170

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX. (WITH TWENTY FOUR TEXT FIGURES.) *William L. Bray* - - - - - - - - - 195

BRIEFER ARTICLES.

NOTES ON TRAVEL. VII. *David G. Fairchild* - - - - - - - 218

CURRENT LITERATURE.

BOOK REVIEWS - - - - - - - - - - - 222

THE SEA BEACH

NOTES FOR STUDENTS - - - - - - - - - 223

OPEN LETTERS.

A CORRECTION. *E. Mead Wilcox* - - - - - - - - - 226

NEWS - - - - - - - - - - - - - 227

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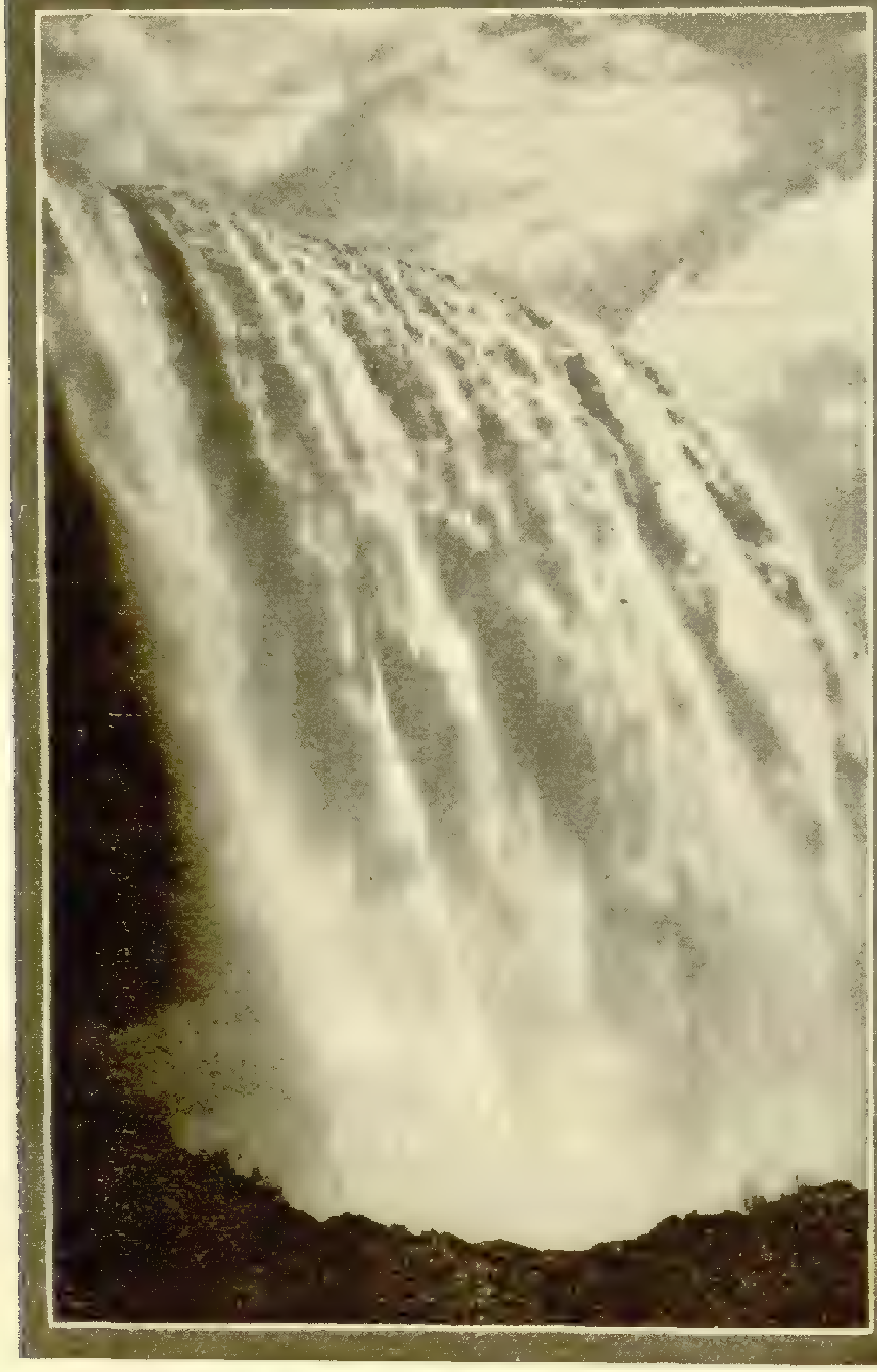

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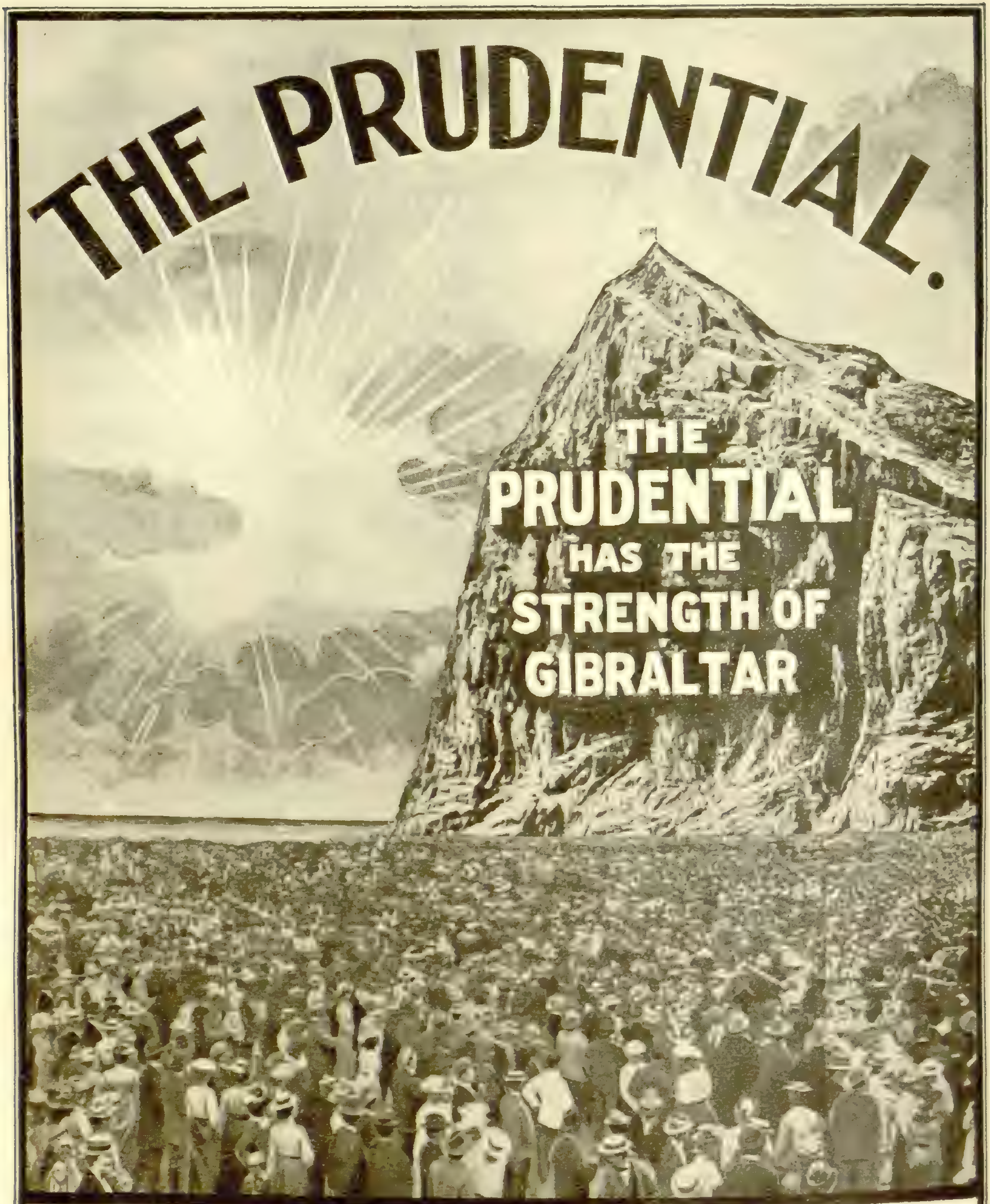
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VOLUME XXXII NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER, 1901

GAMETOGENESIS AND FERTILIZATION IN ALBUGO.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX.

FRANK LINCOLN STEVENS.

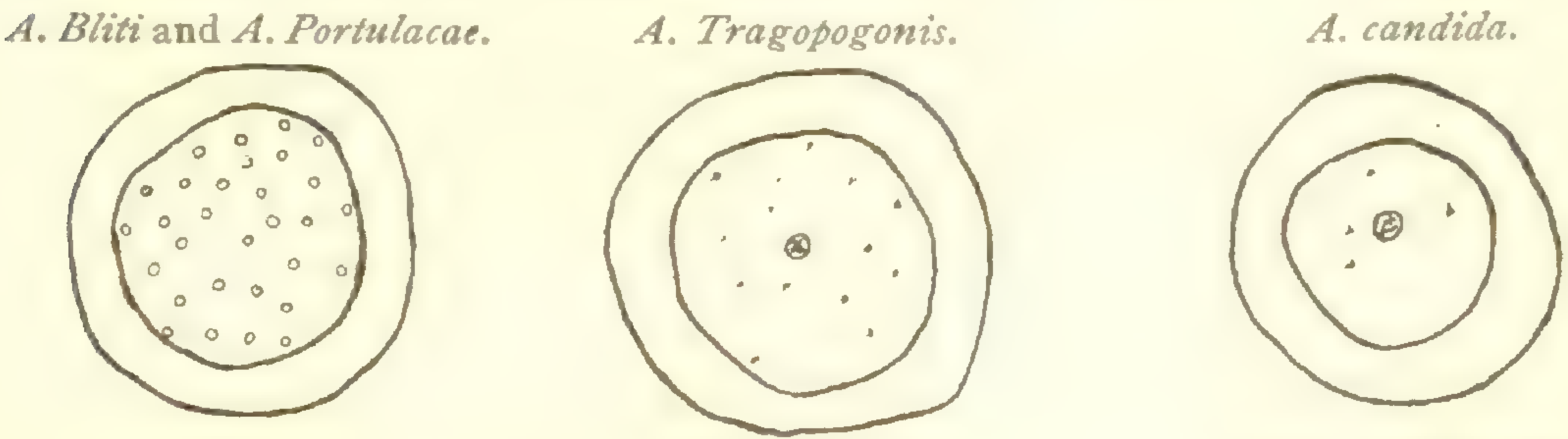
(WITH PLATES I–IV)

[*Continued from p. 98.*]

II. PHYLOGENETIC.

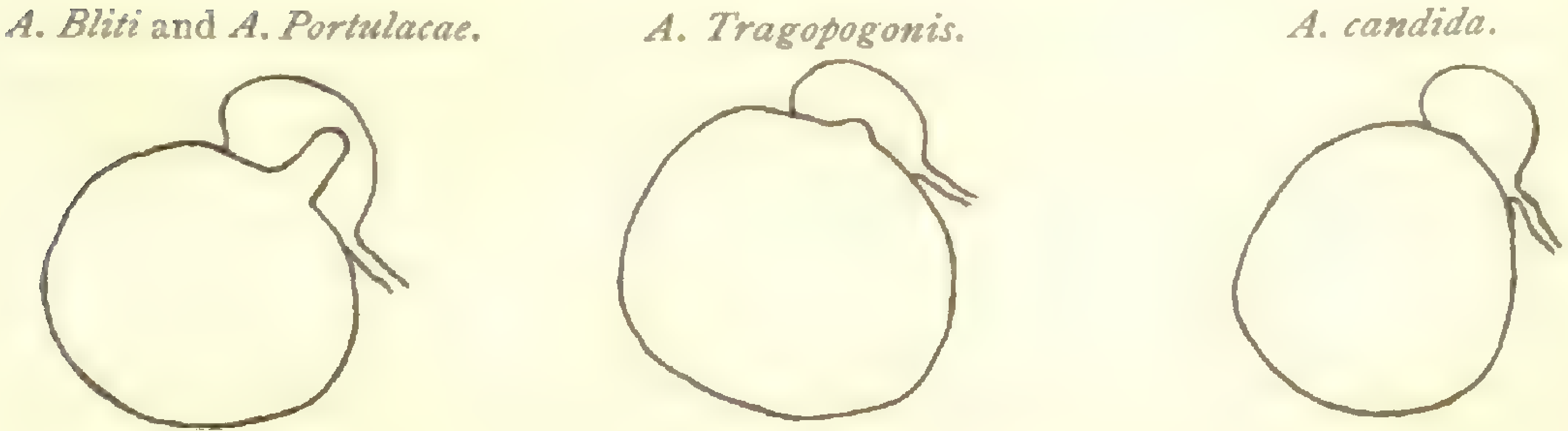
THIS study of Albugo has established a series of forms showing advances in certain respects and a marked reduction in others. The species are closely related, and the difference between two consecutive members of the series is not great, although the extremes are widely divergent. There are four prominent structures or conditions connected with the series, namely, the coenocentrum, the receptive papilla, the mode of zonation, and the number of functional nuclei. Arranged in the order of these characters the species may be listed as *A. Portulacae*, *A. Bliti*, *A. Tragopogonis*, and *A. candida*. In this series the coenocentrum constantly increases in complexity of structure and perfection of function, the receptive papilla becomes less conspicuous, the number of functional nuclei decreases, and the mode of zonation varies in the last two species. These conditions are graphically represented in the accompanying figure which is self explanatory. We may consider the series as a possible expression of the phylogeny of the genus. Which conditions are likely to be primitive?

The coenocentrum increases as the receptive papilla decreases; either one or the other must be retrograding. From a study of these two structures alone it might be difficult to determine the true history, but a consideration of the manner in which the oosphere of *A. Tragopogonis* attains the uninucleate condition shows that this structure in its ontogeny passes through a stage identical with that reached by *A. Portulacae* and *A. Bliti* in their full maturity, thus giving an excellent illustration of the biogenetic law. Both the antheridia and oospheres of *A. Tragopogonis* are multinucleate in their earlier stages, and the development is


A. Bliti and *A. Portulacae.* *A. Tragopogonis.* *A. candida.*

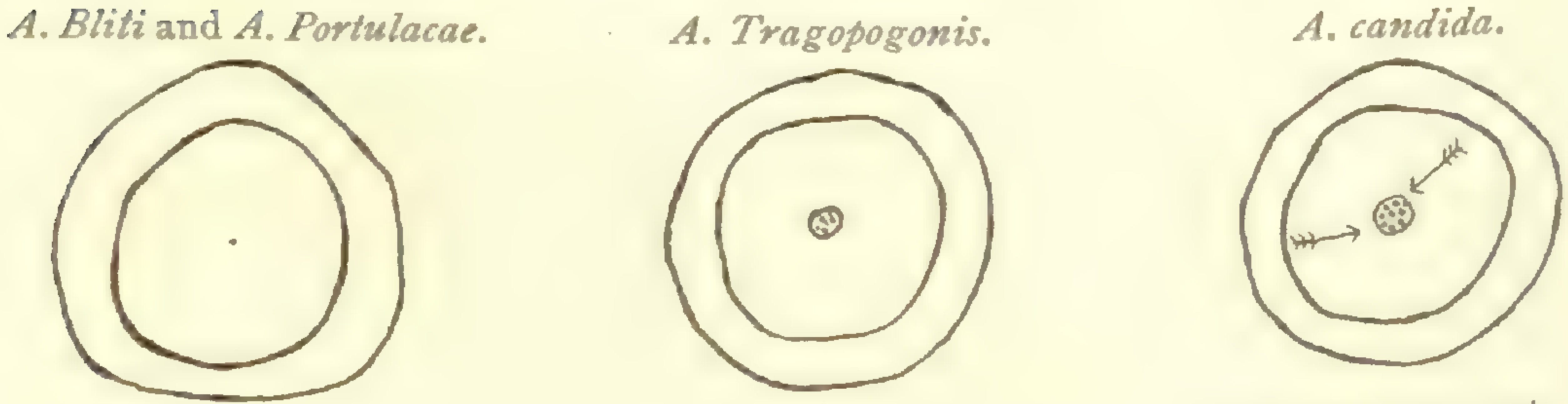
Many functional. Many potential and functional. Several potential and one functional.

NUMBER OF FUNCTIONAL NUCLEI DIMINISHING


A. Bliti and *A. Portulacae.* *A. Tragopogonis.* *A. candida.*

Large. Small. Smaller.

RECEPTIVE PAPILLA DIMINISHING.


A. Bliti and *A. Portulacae.* *A. Tragopogonis.* *A. candida.*

Small. Large, nutritive. Larger, nutritive and strongly chemotactic.

COENOCENTRUM ADVANCING IN STRUCTURE AND FUNCTION.

strictly comparable to that of *A. Portulacae* and *A. Bliti*, stage for stage. Later the supernumerary oospheric nuclei are eliminated, leaving only one female pronucleus to function. It seems necessary, therefore, to regard the supernumerary oospheric nuclei in this species as potential gameto-nuclei, and to regard the uninucleate condition in *A. Tragopogonis* as due to the suppression of the many and the survival of only one gameto-nucleus. In the light of this behavior *A. Portulacae* must be regarded as the primitive form, and *A. candida* the most highly developed. In view of the great functional importance of the coenocentrum in *A. candida* and *A. Tragopogonis*, it is also rational to regard the coenocentrum as an advancing structure. The reverse is true, however, in reference to the receptive papilla, as there is no indication of its present utility, and everything indicates that it is a vestigial structure. The difference in the mode of zonation between *A. Tragopogonis*, where the protoplasm aggregates into preliminary centers which finally coalesce into one, and *A. candida*, where one central region is formed directly by a recession of the protoplasm from the oogonial wall, may well be regarded as an outcome of the reduction of *A. candida* to a uninucleate condition of the oosphere, and may be taken as further evidence indicative of the highly developed rather than the primitive condition of *A. candida*. It is hardly conceivable that evolution could have proceeded in the reverse direction, that is from the type of oogenesis in *A. candida* to that of *A. Tragopogonis*, *A. Bliti*, and *A. Portulacae*. The serial evidence from the coenocentrum, the receptive papilla, the mode of zonation, and the number of functional nuclei concurs in pointing to the multinucleate conditions shown in *A. Portulacae* and *A. Bliti* as primitive, and the uninucleate oosphere of *A. candida* as derived.

The conditions are almost precisely the same as those in the Fucaceae studied by Oltmanns (1889), with the exception that in Albuginaceae and Peronosporaceae a coenocentrum plays an important rôle in the reduction of the number of functional nuclei to its ultimate expression. It is not difficult to imagine that the process of evolution of one form from another may have been very rapid after the development of the nutritive region, the coenocentrum. In *A. Portulacae* and *A. Bliti* the struggle between sister gameto-nuclei is possibly close, but the conditions are quite different in forms possessing a highly developed trophoplasmic area in the center of the oosphere, for it becomes a matter of much importance which nucleus is the first to reach and avail itself of the nutrition. The determining factors may be the position of the nucleus, its orientation, or its sensitiveness to chemotactic influences. In any event, a nucleus which gains more nutrition will contribute its substances to a larger fusion nucleus, and consequently leave stronger descendants to the next generation. Moreover, this action of natural selection, aside from furnishing stronger descendants, will foster exactly those characters which enabled the parent nucleus to prevail in the mother oosphere. In short, a condition obtains here which can easily be conceived as one that would conduce to a rapid evolution from a multinucleate to a uninucleate oosphere through the action of natural selection. It is a manifestation of what Klebahn (1899–1900) has termed "Streben nach Einkernigkeit der Sexualzellen," under such conditions that it is possible to recognize the cause of the "tendency."

A peculiarity, probably a consequence, of the uninucleate condition of the oospore of *A. Tragopogonis* and *A. candida* is the division of its fusion nucleus before the spore passes into the winter condition. A series of mitoses rapidly converts the spore from a uninucleate to a multinucleate structure. The division here, as in many of the higher plants, may be regarded as the initial step in germination. In the species with multinucleate oospores no mitoses occur until the long resting period, normally in this case the winter, is passed. In such forms, presumably the primitive ones, the intrasporal evidence of germination appears when the spore ruptures its coat and manifests externally the new activities. It is clear that the inception of division in one case is homologous with that in the other, and in both it constitutes the commencement of germination. It matters not that in one instance it is before and in the other after the resting period. The divisions which in primitive multinucleate forms come after the resting period have in *A. candida* and *A. Tragopogonis* been transferred to a time before the winter rest. The condition is very similar to that presented in the spermatophytes, where intraseminal germination immediately following fertilization is the rule, although many orchids retain their one-celled condition indefinitely.

Although the division of the fusion nucleus is the first step in germination, the time of this mitosis is subject to variation in different types. The division is delayed in the forms of Albugo having multinucleate oospheres, in *Peronospora parasitica* (Wager 1900), in Saprolegnia and Achlya (Trow 1895 and 1899). The division occurs soon after fusion in species of Albugo having uninucleate oospheres, and in the Peronosporaceae (Berlese 1898). It appears from the consideration of these species that it is not simply a disproportion between the volume of the cytoplasm and the number of nuclei that induces division, for this disproportion is as great in the case of *Peronospora parasitica*, Achlya, and Saprolegnia, as in *A. Tragopogonis*. Wager (1900) has already indicated that in these species, in which the retardation of the fusion is most marked, the inception of division is also most delayed. He says (pp. 275–276):

> *Peronospora parasitica* is at present the only member of the group with retarded nuclear fusion. . . . . In this species it is delayed until the thick zygote membrane has been partly formed. The ripe oospore of *P. parasitica* is uninucleate. . . . . In all the other species of Peronospora which have been examined the ripe zygote is multinucleate.

Similarly, Trow (1895, p. 648, and 1899, p. 175) finds that fusion is slow in Achlya and Saprolegnia, and likewise the division of the fusion nucleus does not occur until after the oospore has passed the resting period. This association of retardation in fusion with delay in division suggests that after the act of fusion is completed, so far as the microscope can give evidence, there may be further changes which the elements of the pronuclei must undergo before fusion is really completed.

The delay of division in species like Saprolegnia, *P. parasitica*, and Spirogyra (Chimelewsky 1888) may be due to a delay on the part of the nuclei in completely preparing for fusion, and to slowness in the act of fusion itself, an act which is not completed when the mere fusion made visible by our present powers of magnification is effected. In this connection Wager (1899, p. 578) makes this suggestion:

> This difference in the behavior of the nucleus during the maturation of the oospore is probably connected with the mode of germination. DeBary has already pointed out that in Cystopus and some other species the oospore on germination produces at once a mass of zoospores. In *Peronospora Valerianellae* and others the oospore at once develops a germ-tube. It may be, therefore, that the uninucleate condition of the zygote indicates germination by a germ-tube, and the multinucleate condition germination by the formation of zoospores.

Apart from the relationships within the group which stand out with more or less clearness, the cytological phenomena emphasize strongly the affinity between the Albuginaceae, Peronosporaceae, and Saprolegniaceae. *Peronospora parasitica*, according to the research of Wager (1900), has a uninucleate oosphere, which is fertilized by the entrance of one antheridial nucleus. In oogenesis the nuclei divide simultaneously while passing to the periphery, as in Albugo, and then one returns to the ooplasm. A highly developed coenocentrum is present, and exerts an attractive influence upon the nuclei even as they lie in the periplasm. All of these conditions, together with the presence of the receptive papilla, clearly attest a relationship between the Albuginaceae and Peronosporaceae. The highly developed coenocentrum and the presence of a uninucleate oosphere indicate that the Peronosporaceae are the more highly developed group. Their ancestors may have been some forms possessing a uninucleate oosphere, similar to that of *A. candida*, from which one of the mitoses has later been suppressed as superfluous. Merely from the evidence of oogenesis, the Peronosporaceae might be regarded as an offshoot from the Albuginaceae after the uninucleate condition had been attained; that is, they may represent a further development of the condition illustrated in *A. candida.* But certain peculiarities of the asexual organs make such a view improbable. The Albuginaceae and Peronosporaceae may both have attained the uninucleate condition of oosphere independently, each being derived from ancestors having multinucleate oospheres. The probability of the multinucleate condition being the primitive one discredits the validity of Fischer's position (1892, pp. 223, 224) regarding the derivation of the Peronosporaceae and Saprolegniaceae from the Chytridiaceae.

Oogenesis in the Saprolegniaceae resembles that in the Albuginaceae in having a multiplication of nuclei through a mitosis, followed by a degeneration of the superfluous nuclei, thus presenting very closely the condition seen in *A. Tragopogonis.* Trow, Hartog, and Humphrey (1892) failed to report a coenocentrum, but Dangeard (1890) has described a structure in both Saprolegnia and Peronospora which may prove to be the same (*cf.* Wager 1896, pp. 308 and 322).

From my own studies, Pythium closely resembles Albugo in its oogenesis. There is a withdrawal of the protoplasm from the oogonial wall, differentiating a vacuolate periplasm, clearly homologous with that of Albugo. Cytological knowledge of the events of oogenesis in this genus will have great value in determining whether its relationship is closest to the Peronosporaceae or Albuginaceae. The present indications favor the Peronosporaceae, where it was placed by DeBary (1881).

Two diametrically opposed processes of oogenesis occur in the single-egged (eineiig) Albuginaceae and the many-egged (vieleiig) Saprolegniaceae. In the first there is a massing of protoplasm in the center, forming the rudimentary oosphere; in the second a peripheral accumulation of protoplasm leaves the central region comparatively free. There is in Peronospora, however, a movement toward the periphery rather than away from it, resembling in this respect Saprolegniaceae. It is conceivable that Pythium may represent a transitional condition between oogonia with single eggs and those with several, which would accord with the theory of DeBary that the Saprolegniaceae evolved through the Peronosporaceae.

The origin of the Peronosporaceae and Saprolegniaceae from lower forms is far from clear. Before the discovery of the multinucleate oosphere in *A. Bliti*, a relation to some type like Vaucheria seemed probable. In Vaucheria many nuclei pass into the rudimentary oogonium, after which, as in *A. candida*, the superfluous nuclei retreat from the cytoplasmic region which is destined to become the oosphere. The essential difference is that in Vaucheria the formation of the wall at the base of the oogonium is delayed until the superfluous nuclei pass back into the parent branch. In the Peronosporaceae the wall is formed when the nuclei are still in the oogonium, thus prohibiting their retreat. The result must be either a multinucleate oosphere or a degeneration of superfluous nuclei. Oltmanns (1895, p. 414) has justly remarked that the condition in Vaucheria is very like that in Fucaceae, presenting only such differences as are necessitated by the presence of cell walls between the oogonium and the parent branch. The remark applies with equal force to the Albuginaceae.

The probability that the ancestors of the Peronosporaceae and Saprolegniaceae had multinucleate oospheres removes these groups from Vaucheria-like forms. If there is any relationship the connection must have been at a time in the ancestry of Vaucheria before the abandonment of the multinucleate condition of its oogonium. As Oltmanns (1895) says, the passage of many nuclei into the rudimentary oogonium in Vaucheria is most readily explicable on the assumption that it once produced many gametes instead of the one that is now habitually found, a view that must meet quite general acceptance, as may be seen from the recent paper of Blackman (1900) and the literature there cited.

Mycologists generally acknowledge the close relationship between the Peronosporaceae, Saprolegniaceae, and Mucorineae. The presence of a multinucleate oosphere and antheridium, and the fusion of two multinucleate masses of protoplasm, quite naturally suggest a possible derivation of the two former groups through the latter. However, as Schröter (1893) has remarked, "Durch das vollständige Fehlen von Schwarmsporenbildung, das oft rein fädige Mycel, die fast nur an der Luft terminal gebildeten Sporen entfernen sich die M. immer weiter von den Algen;" and it is difficult to regard the Mucorineae ancestral to these other Phycomycetes. The manner in which the Mucorineae may have arisen from ancestral algae has been discussed by Davis (1900, p. 308), who has indicated the similarity between the coenogametes of Mucorineae and those of *A. Bliti*. Notwithstanding this similarity it does not seem advisable to regard the Mucorineae as a line productive of such forms as the Peronosporaceae and Saprolegniaceae for the reasons expressed above. The similarity of the vegetative body, however, is sufficient to indicate the possibility, even probability, that the Siphoneae, Mucorineae, Peronosporaceae, and Saprolegniaceae constitute three distinct lines of development from a common parent stock.

Since transition stages in the evolution of these groups are not known, the phylogeny of the coenogamete is little more than a matter for speculation. Two modes of origin are conceivable; either the coenogamete arose from a gametangium producing numerous gametes through the failure of the gametes to separate and become completely individualized; or it may be regarded as a structure, originally multinucleate, which arose and attained sexual differentiation through a line of ancestry composed of multinucleate zoospores.

According to the first view the coenogamete is morphologically a gametangium or physiologically a compound gamete. Each nucleus is the nucleus of a gamete. According to the latter view the coenogamete itself is homologous with a gamete, being a multinucleate gamete. Arguments in support of either view must be based upon such fragmentary evidence as is afforded by the present existing species (which may be made to stand for stages in phylogeny), or the partial repetition of phylogeny through ontogeny. Unfortunately, very little evidence can be expected from ontogeny, since the conditions prevailing during oogenesis are such that any vestigial attempt to individualize gametes from the nuclei would be at once obliterated. Naturally the individualization of gametes would without doubt become quickly eliminated from ontogeny after fertilization *en masse* became a fixed habit. Perhaps some one of the other eight species of Albugo may exhibit in the oogonium vestigial traces of older conditions and a more perfect individualization of gametes, as the conidia in many Peronosporineae develop zoospores which later merge their individuality into a common mass of protoplasm when the conidium germinates by means of a tube. If the multinucleate sex cells were primitively multinucleate, if there has been an independent line of development starting with multinucleate zoospores and leading through multinucleate isogamous gametes to the coenogamete, it might be expected that some structures indicative of such evolution would now be found among living plants. But there are no stages of such a character known, nor is there any group among the algae or fungi which promises to supply them. Possibly the most suggestive group is the Monoblepharadineae, which has recently been investigated by Lagerheim (1899), who finds only one nucleus in the rudimentary oogonium, and as many nuclei in the antheridium as there are sperms to be formed. There is much evidence, however, to support the hypothesis that the coenogamete is homologous with many gametes, which have failed to separate. This hypothesis postulates an origin from uninucleate, swarming gametes, generally present in coenocytic algae, as Hydrodictyon (Artari 1890), Dasycladus (Berthold 1880), Acetabularia (DeBary and Strasburger 1877), Protosiphon (Klebs 1896), not Botrydium (Rostafinski and Woronin 1877) as is so often erroneously cited,[1] thus showing the prevalence of this mode of sexuality among the algae that are usually looked to for the ancestry of the Phycomycetes. The elongation of the sperm nuclei as they lie in the antheridial tube may also be regarded as indicative of an ancestry in which each nucleus was the nucleus of an individual gamete. The fact that Phycomycetes, in conidia and oospores, sometimes lose the ability to individualize their units has an important bearing on the problem. It is well known that the contents of conidia and oospores ordinarily separate into as many regions as there are nuclei, and that these develop into zoospores, each unquestionably an individual. However, if these spores, by a change of external conditions, are induced to germinate by means of a tube, the zoospores do not emerge as individuals. Not merely is there a failure to resolve the protoplasm into individuals, but there is an actual surrender of individuality after it has been attained. Not only does this occur in ontogeny, but it is a very generally accepted belief that it likewise occurred in the phylogeny of this group. In the more primitive forms which germinate by zoospores individualization is not abandoned but is merely delayed, since in germination each fusion nucleus or each of its immediate descendants develops its own plasmoderma and begins independent life. In such form the phenomenon is comparable to delayed wall formation in endosperm, with the remarkable exception that in Albugo fertilization occurs during the period of delay.

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[1] For the most recent work on these species see Iwanoff, 1898.

Pyronema (Harper 1900) may be regarded as an excellent illustration of a condition in which the individuality of the sexual nuclei habitually finds expression only through their behavior in the act of fertilization. The manner in which the fusion nuclei wander away immediately after fertilization, and the absence of units in the cytoplasm, are strikingly similar to Albugo, as are also the mitoses of the nuclei during oogenesis, the marshaling of the nuclei into a hollow sphere, the participation of the oogonium in the dissolution of the wall adjacent to the antheridium ; even the trichogyne resembles in many respects the receptive papilla of Albugo.

While certain Ascomycetes resemble the Florideae more than they do the Phycomycetes, the points of similarity mentioned above between the Phycomycetes, Albugo, and Pyronema, are sufficient to justify careful scrutiny of all features before abandoning the view held by DeBary (1884) concerning the relationship of these two latter groups. Zoosporangia have not yet been studied cytologically with the completeness they deserve, and it is unwise to deny the possibility of relationship between the ascus and the sporangium until both cell and cilia formation in the Phycomycete zoosporangium is understood.

As the conidia in phylogeny and ontogeny stand for zoosporangia, it is clear that they represent masses of potential zoospores, and are consequently synplasts in the sense in which that word was used by Hanstein (1880). The vegetative coenocyte that develops from the spore is also a synplast, which in phylogeny (and often in ontogeny) goes back to a time when each nucleus governed a definite region of cytoplasm. The multinucleate condition of this vegetative body results from a retardation of cell division, similar to that in the embryo sacs, particularly well illustrated in the gymnosperms, and in the eggs of insects (Hertwig 1892). In the latter forms the delay is not maintained long in ontogeny. Cell division follows soon after nuclear division. In the coenocytic algae there is failure to individualize during a whole generation. Existing forms show that the vegetative body was coenocytic long before the gamete became so. In Albugo, the multinucleate condition of the female sexual cell may be regarded as the result of pushing the synplast habit one step further in ontogeny. The sexual cells were the last to give up their individuality, the vegetative cells the first.

The synplast in the Phycomycetes differs from that of most spermatophytes in many ways, most strikingly, however, in the mobility of its potential units. While it is phylogenetically equivalent to many cells, a compound of potential cells, in the sense that Hertwig (1892) uses the expression, the phycomycete synplast, both in sexual and asexual parts, must be regarded as a morphological unit. The potential units have lost their definite limitations and so their morphological value. Discussion regarding the nature of the vegetative coenocyte may be found in numerous texts, as Strasburger (1880, pp. 372, and 1893), Zimmermann (1896, p. 10), Haberlandt (1896, pp. 12–62), Verworn (1897, pp. 74–78), Pfeffer (1897, pp. 49–51). It is unnecessary to quote these authors or repeat familiar discussion here, further than to state that they agree in general with the statement of Pfeffer (1897, p. 51), "Auch derartige Erwägungen zwingen dazu, zunächst den veilkernigen Protoplasten als eine morphologische und physiologische Einheit anzusehen."

There is but little in common between the coenogamete, which is a structure of high physiological efficiency, and such structures as have been described by Golenkin (1900) and Klebahn (1899) in Sphaeroplea, which, as Klebahn remarks, resemble cases of polyspermy. They seem to indicate a pathological rather than a normal condition.

The strict maintenance of the individuality of the nuclei and their characteristic behavior in fertilization adds another strong argument to the evidence, which is becoming cumulatively great, that these structures are the bearers of hereditary characters. The apparent ease with which one nucleus can usurp the cytoplasm of many is an argument against the energid theory of Sachs.

[*To be concluded.*]

BOTANICAL INSTITUTE, BONN.

A STUDY OF THE SPORANGIA AND GAMETOPHYTES OF SELAGINELLA APUS AND SELAGINELLA RUPESTRIS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXI.

FLORENCE MAY LYON.

(WITH PLATES V–IX)

[*Concluded from p. 141.*]

GENERAL DISCUSSION.

CONSIDERING the phylogenetic importance of the group, the literature on the Selaginellaceae is surprisingly scanty. More especially is this true of that which treats of the development of spore and gametophyte. Some marked discrepancies in essential features have appeared in these papers, however, and show how much detailed life histories of more species are needed before further inferences are drawn as regards the relation of this group to others. Only one comparatively full account of a single species has yet appeared, Bruchmann's monograph on *S. spinulosa*, published in 1897, although he gives no account whatever of the development of the male gametophyte nor of the sporangia. He had much difficulty in obtaining normal spores,[1] and therefore was unable to follow the earliest stages of the prothallium in detail. In general, however, he agrees with Heinsen and Arnoldi that there is free cell formation within the spore, followed by periclinal and anticlinal cell walls, thus making a disk-shaped mass of cells in the apical portion of the spore. The upper layers of cells are much smaller and irregularly polyhedral in shape. No diaphragm is formed. Three tufts of trichomes grow from the upper surface of the prothallium, rend the exospore into three flaps along the ridges at the apex, and push them up out of the way of the developing archegonia. Only a limited number of the latter develop, some five to ten as compared with Pfeffer's report of thirty in *S. Martensii*. There are four rows of neck cells, with three cells in each row. Pfeffer reports but two cells in each of the four rows in *S. Martensii;* Campbell reports two in *S. Kraussiana*. Heinsen gives a list of eleven species: *S. Martensii, S. lepidophylla, S. Willdenoviana, S. denticulata, S. apus, S. erythropus, S. Helvetica, S. serpens, S. Douglasii, S. glauca, S. pilifera*, and says that he agrees with Pfeffer on this point. Bruchmann finds that although several embryos may start to grow, but one comes to maturity. The first division of the oospore of *S. spinulosa* is transverse to the axis of the archegonium, and the cell nearer the neck becomes a suspensor.

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[1] "Uber die Keimung der Sporen habe ich zu zwei verschiedenen Malen Versuche angestellt. Das erste Mal sate ich sie gleich nach ihrer Reife (im August) auf Torf aus, hielt sie bestandig feucht und schutzte sie im Winter gegen Frost. Die erste Keimung weniger Sporen dieser Aussaat bemerkte ich erst nach zwei Jahren, weitere keimten dann in dritten Jahre, aber der grosste Teil zeigte selbst nach solcher Zeit keine Keimung."

The most notable fact, however, is that this embryo has no foot. "Ein Fuss in dem Sinne, sie ihn z. B. *S. Martensii, S. Kraussiana* und andere Arten besitzen, fehlt." Whereas, the embryo of *S. apus*, as I have found, has no suspensor. After fertilization the cover cells of the archegonium close together, the walls of the neck cells thicken and turn brown. On the other hand, Pfeffer maintains that the neck of the archegonium of *S. Martensii* gapes widely during the entire embryonic development; and he represents the suspensor pushing up into the neck canal like a wedge. This latter method is the rule in most pteridophytes, and hence *S. spinulosa* together with ~~*S. apus*~~ and *S. rupestris* are exceptions.

In the last twenty years, as far as I know, but four other contributions have been made to a knowledge of these phases of the history of the Selaginellas. In 1871, Pfeffer published his paper "Die Entwickelung des Keimes der Gattung Selaginella." The extreme difficulty of interpreting the spore and prothallial structures, even with the aid of all the modern technique, makes the description given by this author seem an extraordinary performance, and none the less that apparent discrepancies with other species may disappear upon reexamination. His account of *S. Martensii* differs from the foregoing in the following particulars: The megaspore when about one fourth its final size possesses two coats, exine and intine. Against the inner surface of the latter lies a thick layer of protoplasm inclosing a transparent fluid in which floats a large "nucleus." Near the apex "the protoplasm has a different appearance," but he was unable to interpret it. Obviously, he misinterpreted the so-called nucleus, which is the protoplasmic vesicle, and in all probability the peculiar appearance near the apex was due to the presence of the real nucleus. A dome-shaped diaphragm separates the gametophyte into two regions. This he thinks arises at the first division of the spore into two cells. The one toward the apex of the spore becomes subdivided into a tissue three layers thick in the middle, one layer at the periphery. The continuous division of the lower cell fills the basal portion of the spore with larger cells. The hollow spherical portion of the gametophyte below the disk he describes as becoming filled with "freigebildete Primordialzellen." He could not demonstrate the presence of nuclei in these cells, but regards it as probable. According to his statement, the growth of the prothallium occurs at two periods. The disk-shaped mass of cells appears before the spores are shed, the tissue below the diaphragm, the "secondary endosperm," afterward. Archegonia do not develop until the spores fall.

In 1894 Heinsen reexamined the species studied by Pfeffer. He fell into the same error as regards the interpretation of the protoplasmic vesicle and nucleus in the young megaspore. He was unable to determine the origin of the megaspores, other than that a tetrad arose endogenously in the spore mother cell. He denied the existence of a primary and secondary endosperm, and of a diaphragm, and corrected Pfeffer's misinterpretation of the food balls in the gametophyte cavity "as freely formed cells." Infrequently he found the archegonia formed in unshed spores.

The diaphragm which Pfeffer thought was the wall of the first division of the spore Heinsen regards as the plane of separation between the small cells at the apex of the gametophyte and the larger ones below, and not a wall. He also refutes Pfeffer's statement that ultimately the cell divisions completely occupy the basal region of the spore. Heinsen lays great stress on the supposed fact that the nuclei of the Selaginellaceae increase solely by direct division. He investigated material killed at all hours of the day and night, not only spores but vegetative tips, with special reference to establishing this point. He found a total absence of karyokinetic figures. As this statement, which if true would be most surprising, has not been refuted by later writers, it may be of interest to note a possible explanation of the error. In describing his methods of imbedding, Heinsen says that he killed his material by immersing some specimens for ten minutes in Flemming's fluid, others three minutes in a 1 per cent. corrosive sublimate solution, still others "mit gleich gutem Erfolge wante ich ein zweimaliges schnelles Eintauchen in kochendes Wasser an." It is doubtful whether any of the killing fluids thus employed had opportunity to penetrate the sporangium wall in so brief a contact; in which case his material died a lingering death through the washing and dehydrating processes. Under such conditions naturally there would be no traces of karyokinesis. The statement that he had as good results from two quick dips in boiling water as from the Flemming fluid is otherwise inexplicable. It is somewhat difficult to determine whether Heinsen means his statements to be general with regard to all the species he enumerates or not. His summary leads one to assume that the sequence of events there set down is true of the eleven species above named. There are certainly inaccuracies in many details if applied to *S. apus.*

Arnoldi in the *Botanische Zeitung* of 1896 followed in a brief article on "Die Entwickelung des weiblichen Vorkeimes bei den heterosporen Lycopodiaceen." He investigated *S. cuspidata elongata,* and gives a résumé of Heinsen's paper. He agrees with Heinsen on all points, thus reiterating the misinterpretation of the spore content. Campbell in his *Mosses and Ferns*, published in 1895, gives an account of his investigation of *S. Kraussiana*. He too describes "the single large globular nucleus" (*i.e.*, the protoplasmic vesicle) of the megaspore. The diaphragm which exists in this species he explains as arising, not as Pfeffer thought from the first division of the spore, but from the thickening of the walls of the lowermost layer of cells of the disk at the spore apex. He finds "numerous small nuclei" scattered through the protoplasm of the spore cavity, and the protoplasmic layer thickens until it "completely fills the cavity of the spore." I have examined *S. Kraussiana* with reference to these points. The diaphragm is very evident and obviously formed in the manner described by Campbell. I can demonstrate no nuclei at any period in the spore cavity, nor any protoplasm. The protoplasm forms a layer next the wall, as in *S. apus*, and the vacuole within is full of food matter, at first a fluid, then an emulsion, and finally filled with granules and small balls of matter which stain like nuclei. The protoplasmic layer grows thicker, but never fully occupies the interior space as Campbell describes.

The latest contribution is that of Fitting (1900), "Bau und Entwickelungsgeschichte der Makrosporen von Isoëtes und Selaginella und ihre Bedeutung fur die Kenntnis des Wachstums pflanzlicher Zellmembranen." He corrects the error made by each of the above named writers in interpreting the parts of the megaspore. An attempt to discover the exact origin of the megaspores failed, due to the fact that the spore mother cell stained so deeply in all his preparations that the details of the evolution of the four spores could not be made out. He was unable to avoid shrinkage of cells. There follows a very detailed account of the development of the spore coats, in which he differs from Heinsen as regards their origin. He drew conclusions largely from living material examined in a salt solution. As I have said before, the interpretation of the origin of the spore coats seems to me largely a matter of theory, and one who has examined the young spores of *S. apus*, while inclosed in the sporangium and surrounded by sterile mother cells, is skeptical of the results obtained by this method of investigation. He fails to comment on Heinsen's statement with regard to the method of cell division. Both Arnoldi's and Fitting's articles have been comparative studies of certain phases of the Selaginella life history with the same stages of Isoëtes. Thus, until the year 1900 we have not had a correct interpretation even of the parts of the megaspore.

MALE GAMETOPHYTE.—We are indebted to Millardet's memoir for our earliest knowledge of the male gametophyte. This work appeared in 1869, and almost no detail of importance has been added by later workers. In 1885 Belajeff repeated Millardet's work on the same species and corroborated all essential details. There has been no other during the last sixteen years until the present account given in this paper of *S. apus*. How much the discrepancies between the two are due to differences in methods of technique, rather than to specific characteristics, remains to be demonstrated. Millardet and Belajeff both examined the microspores of several species of Selaginella (*S. Kraussiana, stolonifera*, and *cuspidata*) in living condition, then added various reagents to the microscope slide, focusing through the spore coats or crushing them by pressure of the cover glass, to determine the phenomena taking place within. The material for the account of the male gametophyte of *S. apus* was killed, imbedded, sectioned, and stained without removing the spores from the strobilus. It will be seen that the main difference lies in the fact that in the earlier accounts there are eight cells described which constitute an antheridial wall; that later these cells disappear, and the sperm cell complex floats free in the cavity thus formed. Both authors state that they were unable to secure a cellulose reaction for the cell walls. On the other hand, I could demonstrate the presence of no such walls in *S. apus*. The first division of the spore results in two free cells. The first, according to Pfeffer's and Millardet's view, is the reduced vegetative part of the prothallium. The latter, which I have called the generative cell, divides at once into a complex of sperm cells. Is it possible that the protoplasmic films surrounding the vacuoles containing food bodies were mistaken by these authors for cell walls? It is not quite certain that the species of Selaginella called *Kraussiana* in America is the identical one known by that name in Europe. The writer investigated the American form and found the sequence of events identical with those that obtain in *S. apus*. In attempting to repeat the methods employed by Millardet and Belajeff, it was impossible to distinguish through the spore wall the nuclei from the food granules, as both stained alike. Removing the exospore by shoving the cover glass to and fro was a tedious performance, whose results hardly repaid the effort. Moreover, it was impossible to manipulate the stains with enough precision to differentiate the nucleoli. As regards the spermatozoids, explicit statements are few. Belajeff figures those of *S. cuspidata* as biciliate bodies, somewhat elliptical in shape, pointed at the ends, with a slight spiral twist. Millardet gives substantially the same description, but no figures. In connection with his account he makes this reference to the work of M. Roze, who had published his observations in 1864:

> Ainsi qu'on le voit, mes observations sur la forme des anthérozoïdes du *Selaginella Kraussiana* sont loin de s'accorder avec celles de M. Roze sur les anthérozoïdes des *S. Martensii* et *S. Galeottii*. Toutefois, comme il à en affaire à des espèces differentes de celle que j'ai étudiée, je m'abstiens de toute discussion sur ce sujet.

That there existed little information on the subject at this time (1869) is evidenced by the following statement:

> Les seules observations que je connaisse sur la germination des microspores du genre Selaginella sont celles de M. Hofmeister et de M. Roze. Ces deux auteurs se sont bornés à mentionner le fait de la production, dans la spore, de cellules contenant chacune un anthérozoïde. C'est M. Hofmeister qui a constaté le premier l'existence, et la de ces animalcules; M. Roze a montré qu'ils sont biciliés.

So far as I can determine, the authors who have described spermatozoids of named species of Selaginella that they themselves have seen are as follows:

1862. Hofmeister.

1864. Roze first demonstrated two cilia in *S. Martensii* and *S. Galeottii*.

1869. Millardet thus describes the spermatozoids of *S. Kraussiana:*

> Il m'a semblé qu'elle se colore en violet par le chlorure de zinc iodé; je n'ose toutefois l'affirmer. On voit en dedans d'elle un filament roulé en hélice, soit à droite, soit à gauche, de façon à faire environ deux tours complets; l'une de ses extrémités est occupée par le granule réfringent d'amidon que je viens de signaler et par suite extrêmement visible; l'autre est à peine distincte. La première constitue la partie postérieure du corps de l'anthérozoïde, elle décrit un cercle plus étroit que le reste de l'animalcule; on voit d'habitude à côté d'elle quelques granulations à peine appréciables. Les cils semblent placés l'un à côté de l'autre; on les distingue difficilement du corps.
>
> . . . . Ces détails serviront à l'intelligence des différentes formes des spermatozoïdes. Dans leur état de développement complet, ils sont entièrement débarrassés de leur vésicule et de la membrane de leur cellule mère, et présentent à l'extrémité postérieure un corpuscule d'amidon; il est resté dans la vésicule où on le retrouve; c'est là une seconde forme. Une troisième est constituée par les animalcules qui portent avec eux une vésicule; une quatrième, par ceux qui ne sont qu'incomplètement dégagés de leur cellule mère.
>
> Dans la forme la plus dévéloppée, le corps est presque droit et décrit une spirale à peine sensible. Sa longueur dans cet état est 0.018 ^{mm} environ. Il s'amincit graduellement depuis l'extrémité postérieure jusqu'à la naissance des cils: son épaisseur maximum ne dépassé pas 0.0007 ^{mm} environ. En avant il se bifurque et se termine ainsi par deux cils très-tenus, deux fois aussi longs le corps.

1871. Pfeffer described the male gametes of *S. Martensii*, and *S. caulescens*.

1885. Belajeff examined *S. cuspidata*, *S laetevirens*, *S. Martensii*, *S. caulescens*, *S. stolonifera*, *S. Kraussiana*, and *S. Poulteri*. Of these he gives figures only of the spermatozoids of *S. stolonifera*.

Thus, in the thirty-nine years since the speramatozoids of the Selaginellaceae were first described, there have been only four contributions upon the subject in which the spermatozoids of but eight species are described from direct observation vouched for by the writer.[3] The difficulty of determining the structure of bodies so extremely small can hardly be overestimated.

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[3] 1. *S. Martensii:* Roze, 1864; Pfeffer, 1871; Belajeff, 1885.
2. *S. Galeottii:* Roze, 1864.
3. *S. Kraussiana;* Millardet, 1869; Belajeff, 1885.
4. *S. caulescens:* Pfeffer, 1871; Belajeff, 1885.
5. *S. cuspidata:* Belajeff, 1885.
6. *S. laetevirens:* Belajeff, 1885.
7. *S. stolonifera:* Belajeff, 1885.
8. *S. Poulteri:* Belajeff, 1885.

With either a Bausch & Lomb $\frac{1}{12}$ oil immersion objective and $\frac{3}{4}$ ocular, or a Zeiss oil immersion 2^{mm} and ocular 3, I was able to make out the spermatozoids only by their characteristic rotary movements as they left the microspore of *S. rupestris*. Their spiral form and attached vesicles were facts determined rather by interpreting appearances by those I had definitely seen in apparently similar but larger bodies, than by actual observations. The spermatozoids of *S. apus* are somewhat larger, and I feel that there is less likelihood of error in describing them. It is obvious that a more critical examination of many species is needed before much weight be placed upon the so-called aberrant forms of the Selaginella spermatozoids in tracing the phylogeny of the group.

THE DEVELOPMENT OF THE SPORANGIA.—The two most recent and important papers on the development of the sporangium are Goebel's (1880) and Bower's (1894). I shall quote verbatim Bower's summary of results from Selaginella:

1. The sporangium is eusporangiate, and arises from the tissue of the axis, above the subtending leaf; the position varies in different species.

2. The origin of the sporangium is similar to that of Lycopodium, and especially resembles *L. inundatum*, to which species the mature sporangium also is similar in form.

3. Two primary archesporial cells are usually present in each radial section, and these are derived, as in *L. inundatum*, from segmentation of two distinct cell-rows; as seen in tangential section, the archesporium is referable to three or four such cell-rows.

4. The first periclinal divisions in these cell-rows do not always define the archesporium finally; subsequent periclinal divisions may result in addition to the central mass, as has been proved for Equisetum; but here the addition is less regular.

5. The tapetum results from tangential division of the outermost cells of the central mass; the greater part of it originates as described by Goebel.

6. The tapetum is thus a sterilized part of the potential sporogenous tissue; a further example of sterilization is seen in the megasporangium, where all the sporogenous cells are disorganized, excepting the one mother cell of the megaspores.

7. Abortive sporangia are to be found at the base of the strobilus as in many species of Lycopodium.

With regard to the derivation of the sporogenous tissue, repeatedly radial sections show a distinct plane of segmentation separating the sporogenous tissue into two such definite regions that it is difficult to avoid the conviction that each complex is the progeny of two independent cells. The term "archesporium" is used by Bower to signify the lower cell or cells. I have used the term to indicate the superficial cell itself. With regard to the fourth statement, my observations on *S. apus* do not agree. With the fifth and sixth statements, as regards the origin of the tapetum, my observations are in accord. The seventh statement I find true of *S. rupestris*, but not of *S. apus*.

In no particular do my preparations agree with Campbell's figures of the sporangial development of *S. Kraussiana*.

Of no little interest is the incomplete septum in the microsporangium of *S. rupestris*, which arises above the pedicel. In vertical section, the resemblance to the celebrated fossil *Lepidodendron Braunii*, as figured by Bower (see his *plate 48, fig. 100*), is very marked. He discusses in the accompanying text the possible function of this region of the sporangium. "Possibly," he says, "these extensions of sterile tissue may have facilitated the nutrition of the developing spores, or they may perchance have contributed to the mechanical support of the sporangial wall." In connection with the former theory, it is noteworthy that this septum is found only in the microsporangium, where some of the spores are remote from the tapetum. A feature that may have some bearing on this point is the fact that the megaspore mother cell, so far as I have observed, is always near the periphery of the sporogenous mass and never at the center, a favorable position to secure nutrition from the tapetum. Scott in his *Studies in fossil botany*, 1900, says, *à propos* of this feature in *Lepidostrobus Veltheimianus*, "this structure may be compared with the trabeculae of Isoëtes. It is best shown in the microsporangium, but may have originally been present in the megasporangia also."

Of even greater interest is the simultaneous discovery of a paleozoic lycopod each of whose sporangia contains a single megaspore or embryo sac, which presumably was fertilized while still attached to the plant, with the condition that I have described above that obtains in *S. rupestris* and *S. apus*. Of the integument that grows up about the sporangium of the *Cardiocarpon anomalum*, described by Scott, leaving at the top an open slit-like micropyle, there is no trace I think, except that in *S. rupestris*, quite late in the development, after the embryo has formed, the megasporangium becomes sunken in a shallow pit formed by the cushion-like upgrowth of the sporophyll around the pedicel. This outgrowth hedges in the ligule with the sporangium, and may be homologous with the Lepidostrobus integument. Scott's statement, therefore, that "the recent discovery of Lepidostrobi with integumented, seed-like sporangia, in which only one megaspore came to perfection, shows that some paleozoic members of the group went far beyond any of the living representatives in the differentiation of their reproductive organs," needs modification in view of the fact that *S. rupestris* normally at the present day produces seed-like sporangia with well developed embryos.

SUMMARY.

1. In both *S. apus* and *S. rupestris* the sporangium frequently, if not always, may be traced to a single superficial cell, the archesporium.

2. The sporogenous tissue may arise in two ways. First (*S. rupestris*), from the single hypodermal cell formed by the archesporium being divided by a periclinal wall, thus producing a wall and a sporogenous cell. Second, by the archesporium (which in this case is assumed to consist of two independent superficial cells) dividing into four cells by a periclinal wall, the two hypodermal cells thus formed developing the sporogenous complex. In each case the epidermal cells form the sporangium wall. It is possible but not demonstrated that the second case may be a phase of the first wherein the original superficial archesporial cell divided by an anticlinal wall.

3. The tapetum is formed in part from the sporogenous cells near the exterior of the mass, and in part from adjacent vegetative cells which come to form a more or less regular layer. It is defined very early, and is active and glandular up to the period that the spores have attained their full size, then becomes reduced to a thin epithelial-like layer lying against the sporangium wall.

4. Microsporangia and megasporangia are indistinguishable before the spore mother cells are differentiated. At this stage, in the case of the megasporangium, one or rarely two cells become more conspicuous and divide into spores. If microspores are to be formed, the majority of the cells continue dividing. After the megaspore mother cell is differentiated, all other cells in the megasporangium cease dividing.

5. In *S. apus* four megaspores arranged tetrahedrally are formed within the spore mother cell. In *S. rupestris* four spores may develop in the same manner, only one or two of which may come to maturity; or, most commonly, there may be but a single division of the mother cell nucleus, in which case there are but two spores formed; or again, there may be a redivision of one only of the two daughter nuclei, resulting in three spores of which only one or two attain maturity. Isolated cases have been met with where but one megaspore was formed. As there were no signs of other aborted spores, presumably the megaspore mother cell never divided, but became directly the single megaspore. In no case have more than two spores in a single megasporangium been found which were fertile, and very frequently only one.

6. The megaspore of each species has three distinct coats, the exospore, mesospore, and endospore. The former originates on the inner face of the spore mother cell membrane, and when first distinguishable is a film of unequal thickness. This either directly or indirectly gives rise to the exospore. A thick layer develops between the exospore and the protoplasmic vesicle, which later in its history separates into two layers, the mesospore and the endospore.

7. The female gametophyte is formed by free cell division of the megaspore, the nuclei dividing by indirect division. These nuclei are confined to the apical portion of the spore. Several layers of nuclei are formed by repeated tangential and radial divisions so that there are six or seven in the apical region and one in the basal. Areas of cells are blocked off by protoplasmic radiations passing from the apex outward and inward. The walls of the cells are produced by nuclear plates in the final division. There is no diaphragm, and at no stage of its development are there nuclei in the lower or the central portions of the gametophyte, which at first contains liquid, and finally a semisolid mass of granular matter.

8. A cushion of cells protrudes through the tripartite cleft in the exospore at the apex. From cells in the upper row of this cushion a limited number of archegonia develop. The cells of this region are markedly smaller than those in the other regions of the gametophyte. No part of the archegonium protrudes from the general level except the cover cells.

9. The megaspores and gametophytes are nourished by matter secreted by the tapetum and passed through the spore mother cell membrane, which persists until the spores are nearly half grown.

10. The microspores develop in a fashion analogous to the megaspore. A large percentage of the mother cells form tetrads, the largest proportion of which are aborted at this stage.

11. The male gametophyte of *S. apus* consists of a single prothallial cell and an ovoid naked mass of potential sperm cells arranged in two groups. There is no antheridium, nor is there a wall which separates the prothallial from the sperm cells.

12. The spermatozoid of *S. apus* is a spirally coiled body; that of *S. rupestris* is of similar shape but much smaller. The presence of cilia in either was not demonstrated.

13. The megasporangia and microsporangia of both species open by definite lines of dehiscence.

14. Fertilization in both species occurs while the spores are

unshed and the sporangia are still attached to the strobilus. At this period the strobilus ceases to form new sporangia. The strobilus of *S. rupestris* retains its physiological connection with the plant until the embryo has produced cotyledons and a root.

15. In the early autumn *S. apus* sheds all strobili whether fertilization has occurred or not. *S. rupestris* retains its stroblii throughout the winter and fertilization occurs in the spring.

16. *S. apus* forms twelve to fifteen megasporangia in each strobilus, all of whose spores are generally fertile. The comparatively limited number of embryos formed is due probably either to the limited number of fertile microspores, or to mechanical difficulties in the way of fertilization, possibly both. *S. rupestris* produces strobili far in excess of the number of purely vegetative branches, the majority of which develop only sterile spores except under very favorable conditions. The sterile spores are shed profusely during the summer, and the strobili which remain on the plant throughout the winter retain their power of apical growth. The first sporangia formed in the early spring contain microspores. There is but a limited number of these ; then follows under favorable conditions either fertilization or the development of megasporangia, which continues until checked by the development of embryos in the older regions of the strobilus, or in case fertilization fails by the approach of winter.

TECHNIQUE.

The tender tips of the strobili offer no special difficulties in preparation for the microtome, but the older sporangia, especially the closely compacted strobili of *S. rupestris*, are exceedingly resistent to the entrance of reagents, and the hardened epidermis of the sporophyll, combined with the thick walls of sporangia and spores, render sectioning difficult. Certain stages of the spores are peculiarly liable to collapse. These technical difficulties probably explain many gaps in our knowledge. The following method was followed in preparing the material for this investigation.

KILLING AGENTS.—Flemming's weaker fluid, Hermann's chromacetic acid, and bichromate of potassium combined with acetic acid, gave the best results. Corrosive sublimate, absolute alcohol, picric acid, Merkel's and Perenyi's fluid were tried, but the results were unsatisfactory in that I failed to get such successful staining after their use.

These fixing fluids were used boiling hot. In the case of the Flemming, the chromic acid and water were brought to the boiling point, the osmic and acetic acids quickly added and the mixture poured over the strobili which had previously been removed from the plants. The vessel was covered tightly and the contents allowed to cool gradually to a temperature of 30° C. The spores were fixed in twenty four hours, but often were left in the killing fluid two or three days with no deleterious effects. Water of approximately the same temperature (30° C.) was used for washing, in very large quantities, and changed frequently for two days. Sometimes it was more convenient to use cold running water, in which case three days' washing was necessary to remove all acid. The dehydrating process was equally gradual: twelve hours each in 10 per cent., 20 per cent., 30 per cent., 50 per cent., 75 per cent., and 80 per cent. alcohol respectively. In 95 and 100 per cent. three days each, and the alcohol changed each day. Xylol was added to the specimens with even more caution, as an examination of material from day to day during these manipulations disclosed the fact that at this point danger of collapse was greatest. Six intermediate grades between absolute alcohol and pure xylol were employed, each for twenty-four hours. The strobili remained in pure xylol until they became transparent, which frequently was not for a week, dependent upon the age of the spores. When this condition was obtained, the xylol was replaced by fresh, and small bits of soft paraffin (melting point 30° C.) were added gradually as long as they would dissolve at the temperature of the room. This usually required two days. Thence the vessel was removed to the bath (temperature 40° C.), which was raised slowly to 54° C., soft paraffin being added during the time up to the point of saturation. At this time the cover was removed from the vessel to facilitate the evaporation of the xylol, and harder paraffin added in small quantities at intervals. At the end of two or three days the temperature was raised to 65° C., and maintained for one week, after which time the xylol had evaporated, and the strobili were infiltrated with paraffin.

At first, on the supposition that such protracted exposure to reagents and heat would injure the more delicate very young sporangia, the tips of strobili were removed, carried through the various media in much less time, and subjected to a temperature of 50° C. for about ten hours only. Comparisons later showed that these precautions were unnecessary, and that the longer exposures produced better results, even in the apical cells. Moreover, having a strobilus cut *in toto* was of the greatest value in interpretation. Further experiments prove that considerable latitude in the direction of longer periods of immersion in the various fluids are not injurious, but all attempts to hasten results by shorter exposure than the period stated above were unfortunate. By an oversight, at one time the temperature rose in the bath three successive nights to 75° C., but with no injurious effects. Some difficulty was experienced in imbedding. The paraffin was inclined to shrink away from the rough surface of the spore wall, which caused the sections to drop out of the paraffin ribbon when transferred to the slide. The difficulty was overcome by removing the strobili to the imbedding dish from the bath, letting them cool off slightly (to about 40° C.), pouring on paraffin at a temperature of 80° C., then cooling as rapidly as possible in ice water. No further trouble was experienced and the strobili could be sectioned without difficulty.

STAINS.—The best stains for the youngest stages of sporangia are iron haematoxylin (Haidenhain method), and the so-called Flemming triple stain—saffranin, gentian-violet, and orange G. Frequently gentian-violet and orange G were employed without saffranin; for the gametophyte development, after the appearance of the proteid matter in quantities that obscured the other cell features, cyanin and erythrosin, after treating the sections on the slide with dilute sulfuric acid and chloroform, produced very satisfactory results. The power to take up the stains was retarded in the case of the proteid granules, whereas the nuclei and cell walls were more readily and more brilliantly dyed after this treatment. Karyokinetic figures were especially clear.

It remains my pleasant duty to express my thanks to Dr. John M. Coulter, and to other members of the Botanical Department of the University of Chicago, for many suggestions offered in the course of this investigation. To Mr. E. J. Canning, Head Gardener of the Botanic Gardens of Smith College, I am deeply indebted for aid in collecting and growing material.

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EXPLANATION OF PLATES V–IX.

All figures were drawn with the aid of a camera lucida and a Bausch and Lomb microscope, and were reduced to one fourth their original size in reproduction.

PLATE V. Selaginella apus. Oc. ¾, oil immersion $\frac{1}{12}$.

Fig. 1. Vertical median section of tip of strobilus showing the apical cell, a young sporophyll whose apical cell is just established, an archesporial cell (shaded), and a two-celled sporophyll (distinguished by black nucleoli).

Fig. 2. Radial section of portion of strobilus showing sporophyll and two superposed cells (shaded), resulting from a transverse division of the archesporial cell. The superficial cell by repeated division in one plane

eventually forms the initial sporangium wall. The hypodermal cell is the initial sporogenous cell. The first cell of the ligule is distinguished by a black nucleolus.

FIGS. 3 and 4. Radial section of portion of strobilus showing two superficial archesporial cells (shaded).

FIG. 5. Radial section of strobilus showing three-celled sporophyll (near apex), a two-celled sporangium (shaded) near the base of the subtending sporophyll, and the early stage of the vascular system.

FIG. 6. Radial section of strobilus showing four-celled sporangium possibly formed by two archesporial cells which divided by transverse walls. A stage subsequent to *figs. 3* and *4*.

FIG. 7. Radial section of older sporangium. Sporogenous cells are shaded, and are represented with black nucleoli.

FIG. 8. Vertical section of sporangium showing definite radial arrangement of cells and plane of cleavage dividing it into two groups of cells, each the progeny of one of the two superficial archesporial cells shown in *figs. 3* and *4*.

FIG. 9. Vertical median section of sporangium more advanced. Sporangium wall at this stage consists of one layer.

FIG. 10. Median transverse section of sporangium showing the sporangium cells, the tapetum, the inner and the outer layers of the sporangium wall.

FIG. 11. Section of sporangium after the spore mother cells are established. In this stage the sporogenous cells are distinguished by two conspicuous masses of granular matter which lie against the nucleus.

FIG. 12. Group of sporogenous cells in synapsis stage. Probably microspore mother cells.

FIG. 13. Detail of small portion of megasporangium showing megaspore mother cell (distinguished by the lumps of matter on either side of the nucleus) lying near the glandular tapetal cells. Two sterile sporogenous cells are at the left and below the megaspore mother cell.

FIGS. 14–24. Stages in the development of the megaspores. *Fig. 16* shows the characteristic sextuple spindle stage previous to the separation into spores, as seen in *fig. 18*. The four nuclei pass from the bases to the apices of the newly formed spores, as shown in *figs. 18–22*.

FIGS. 25–28. Details of cell division in the final stages of development of the female prothallium. *Fig. 25* represents a portion of a section of the stage represented in *fig. 49* to show thickness of protoplasmic vesicle and the invasion of fibrillae blocking off the separate nuclei.

FIG. 29. Section of archegonium. The egg and ventral canal cell are lying in a plane perpendicular to the long axis of the archegonium. The egg is the larger cell with black nucleus.

FIG. 30. Section of archegonium in which the egg lies below the ventral canal cell, and the neck canal cell above it. Two tiers of neck cells are drawn.

FIG. 31. Stage younger than that shown above, before neck cells are cut off.

FIG. 32. Archegonium with egg and ventral canal cell laterally placed. No trace of neck canal cell. Neck consists of four tiers of cells, each tier comprising an upper (superficial) cover cell, and one neck cell. The cells abutting on the venter belong to the prothallium.

FIGS. 33 and 34. Mature archegonia. In *fig. 33* a spermatozoid is lying on the receptive spot of the egg. *Fig. 34* shows a one-celled embryo.

PLATE VI. Selaginella apus. Oc. 2, oil immersion $\frac{1}{12}$.

FIG. 35. Section of young megasporangium at earliest stage when megaspore mother cell is distinguishable from sterile cells. For detail see *fig. 13*.

FIG. 36. Section of older stage of megasporangium. Megaspore mother cell has moved near center of sporangium.

FIG. 37. Oblique section of megasporangium showing young tetrad, and sterile mother cells, floating in slime composed in part of disintegrated sterile cells and in part of a secretion poured out by tapetum.

FIG. 38. Section of somewhat older stage of megasporangium containing group of four megaspores (only three are represented). Each spore consists of an outer coat, the exospore; a median layer which is later differentiated into the mesospore and the endospore; a vesicle of protoplasm containing a limpid fluid and possessing a very small nucleus. The spaces intervening between vesicle and median layer and between the latter and the exospore are filled with fluid.

FIGS. 39–41. Successive serial sections of a tetrad, to illustrate the fact that the exospore is a continuous envelope common to the group of spores and splits as they move apart.

FIG. 42. Section of group of megaspores but little older than those in *fig. 38*. Filamentous processes shown between spores. The mother cell membrane, beyond whose boundary the radiations do not pass, envelops the tetrad.

FIG. 43. Section of two megaspores more advanced. The spore at the left is cut nearly in half from apex to base, that at the right is a slice across the apex. Protoplasmic vesicle grown but little larger than in *fig. 42*. Spine-like processes upon exospore in connection with radiations. Mother cell membrane still evident.

FIG. 44. Section of the female gametophyte showing the protoplasmic vesicle with two nuclei. The radiations extend across the spaces between vesicle and median layer, between median layer and exospore, and between the latter and the original spore mother cell membrane.

FIG. 45. Section of female gametophyte whose vesicle has five nuclei and no cell walls. The exospore has grown to the size of the megasporangium as shown in *fig. 38*. The median layer has divided into the endospore (represented in section as a broad black band), and the mesospore which can be distinguished only as a delicate layer (represented by a single line) just without the endospore. The exospore is of spongy appearance and is still in contact with the persistent spore mother cell membrane. Fluid, presumably protoplasmic in nature, fills intervening spaces.

FIG. 46. A transverse median section of a female gametophyte in "film" stage. The megaspore, endospore and protoplasmic vesicle (studded in its apical region with large free nuclei) have stretched to the dimensions of the exospore, against whose inner surface they form a layer consisting of three delicate lamellae. The central vacuole is filled with clear fluid. The same stage is shown in *figs. 47* and *48* the former representing a surface view, the latter a median section.

PLATE VII. Selaginella apus.

All figures except 56 and 58 drawn with oc. 2, obj. ⅙. *Fig. 56* is drawn with same combination as plate V; *fig. 58* with oc. 2, obj. ⅔.

FIG. 47. Surface view of the protoplasmic vesicle as if seen through spore walls.

FIG. 48. Vertical median section of the same stage. The nuclei are massed in the apical region and the interior of the vesicle is occupied by a vacuole.

FIG. 49. Surface view of the gametophyte at the moment when protoplasmic fibrillae appear in the apical region and radiate over the surface of the gametophyte. The nuclei in the lower part of the figure are in process of division. The vesicle has increased in thickness (cf. *fig. 50*), and is beset with proteid granules. Contents of vacuole a homogeneous liquid.

FIG. 50. Median section of same.

FIG. 51. Median vertical section of female gametophyte. Protoplasmic vesicle much thicker in apical region where the nuclei are disposed in several layers diminishing to a single one in the equatorial region. Fibrillae permeating the nucleated portion have outlined indefinite areas but there are no cell walls. Contents of vacuole an emulsion.

FIG. 52. Section showing a portion of the megasporangium with female gametophyte *in situ* to show the differentiation of the wall. In the lowermost part of the figure the fragile cells of the area of dehiscence are seen in cross section. The inner layer of the wall probably supplies the outer with nourishment. The vestiges of the tapetum are upon its inner face, as a pavement layer, and a few sterile mother cells lie at the left next the wall.

FIG. 53. Vertical median section of female gametophyte showing the differentiation of cells into an apical superficial layer from which develop

archegonia, and a lower vegetative region. The delimitation of the archegonial region is shown by the trefoil shaped cleft seen in the lowermost spore of *fig. 58*.

FIGS. 54 and 55. Section of female gametophyte showing archegonia. Details of the process of division in the unshaded cells of *fig. 54* are represented in *figs. 26–28*.

FIG. 56. Two embryos, one of two cells, the other of three, lying side by side in one venter. All walls shown are parallel to the axis of the archegonium. Compare relative position of these embryos with that of the egg and ventral canal cell in *figs. 29, 32*.

FIG. 57. Embryo *in situ*. The root lies toward the apex of the gametophyte. At the right the club-shaped foot of large cells is embedded in the prothallial tissue. The embryo is bent with respect to its long axis so that the stem apex and cotyledons are brought nearer the root than appears in the drawing, which is a reconstruction from serial sections. The two leaves with their relatively large ligules are developed successively and envelop the tip of the stem (shown by dotted line). The embryo is still within the spore wall and sporangium.

FIG. 58. Vertical section of megasporangium containing three female gametophytes. The lowermost shows the trefoil-shaped cleft in the apical region of the spore wall, exposing the archegonia. The two other oblique sections are not so advanced in development. The pad of tissue at the base of the sporangium lies above a region of storage cells in contact with the vascular bundles of axis and sporophyte.

PLATE VIII. Selaginella apus.

All drawings made with oc. $\frac{3}{4}$, oil immersion, obj. $\frac{1}{12}$, excepting 60–62. Figs. 60, 61 were drawn with oc. 2, oil immersion, obj. $\frac{1}{12}$. Fig. 62 with oc. $\frac{3}{4}$, obj. $\frac{2}{3}$.

FIG. 59. Section of microsporangium, showing microspore mother cells, tapetum, inner and outer layers of sporangium wall.

FIG. 60. Median vertical section of microsporangium with mother cells in synapsis stage. Sub-archesporial pad developing at base of sporangium.

FIG. 61. Slightly oblique section of microsporangium showing microspores in groups of four (tetrads).

FIG. 62. Median vertical section of microsporangium to show sporangium wall at maturity. Dehiscence region cut across at apex. Sporangium opens in two valves, the subarchesporial pad at top of pedicel serving as a fulcrum.

FIGS. 63, 64. Microspore mother cells during first division of nucleus.

FIGS. 65, 66. Sextuple spindle stage with nuclear plates.

FIG. 67. Exterior view of young microspore.

FIG. 68. Section of tetrad, showing continuity of exospore around the four microspores, and spore mother cell membrane enveloping the tetrad. The protoplasm is a thin vesicle with a single nucleus, parietally placed, and surrounding a large central vacuole.

FIG. 69. Exterior view of mature microspore showing pebbled exospore.

FIG. 70. Vertical section of male gametophyte after first division of spore into generative and vegetative cells.

FIG. 71. Male gametophyte as seen by focusing through spore coats. The large generative nucleus lies near the wall, the vegetative cell not in focus.

FIG. 72. Male gametophyte showing generative cell in section.

FIG. 74. Male gametophyte showing lenticular vegetative cell at left. The remainder of the content constitutes the generative cell with a centrally placed nucleus. Masses of deeply staining proteid matter appearing.

FIG. 75. Section of male gametophyte in which masses of proteid matter have increased in number. Vegetative cell appressed to wall at left.

FIG. 76. The protoplasm is aggregated around the centrally placed generative nucleus and has sent out radiating processes, connecting it with a peripheral layer. The vacuoles thus isolated are filled with a semi-fluid granular matter.

FIGS. 77, 78. A common appearance, where a large symmetrical mass of proteid matter (solid black) in the central vacuole may be mistaken for a nucleus.

FIG. 79. First division of generative nucleus. Persistent vegetative cell appressed to wall in lower portion of figure.

FIGS. 80–87. Phases of the early divisions leading to the spermatozoid mother cells.

FIGS. 88–95. Sections in various planes showing the two cell complexes and their relation to the dissolving proteid masses by which they are enveloped. The masses of food matter are separated by strands of protoplasm in *figs. 88, 93, 95.*

FIG. 96. Exterior view of male gametophyte displaying trefoil shaped cleft in apical portion. The complexes of spermatozoid mother cells protrude through the gap.

FIG. 97. Male gametophyte with spermatozoid mother cells as seen by focusing through spore coats. The unusually persistent vegetative cell is represented lying above the mother cells.

FIGS. 98, 99. Male gametophyte at maturity. The endospore protrudes like a short pollen tube through a gap on the ruptured exospore, and contains a slimy homogeneous fluid which later is discharged with the spermatozoids.

FIG. 100. A transverse section of a female gametophyte displaying the

eggs and spermatozoids. The necks of the archegonia have been sliced off somewhat obliquely.

PLATE IX. Selaginella rupestris.

FIG. 101. Apex of a strobilus in radial section. A single archesporial cell (shaded) at the base of a sporophyll. The cell with black nucleus is the initial cell of the next younger sporophyll of the same rank.

FIG. 102. First division of archesporial cell into a hypodermal and a superficial cell.

FIG. 103. The superficial cell of the first division has divided into three wall cells, and the hypodermal cell into two sporogenous cells, forming a wedge-shaped mass.

FIG. 104. Radial section of portion of strobilus. The largest sporophyll has ceased to grow at the apex which is converted into a branched spine. The initial cells of the ligule at the base of the sporophyll are represented with black nuclei. The tissue is rupturing to form air chambers in the basal region. The sporangium has been outstripped in growth by the sporophyll next above it. The two shaded cells in the upper part of the figure represent the same stage of sporangium as seen in *fig. 102*.

FIG. 105. Section of sporangium. The wall is nearly completed and the tapetum is becoming differentiated from the sporogenous complex of cells. The limits of the latter in the basal region not so clearly defined as represented in the figure.

FIG. 106. Detail showing two megaspores and several sterile mother cells.

FIGS. 107–117. Phases undergone by megaspore mother cells preceding divisions into spores.

FIG. 118. First division of megaspore mother cells into two spores.

FIG. 119. Section through sister megaspores. A portion of the sculptured exospore is removed from the upper surface of each, showing the protoplasmic vesicle with a small nucleus floating in liquid. The spore mother cell membrane envelops the two spores.

FIG. 120. Section showing incomplete division of the protoplasm of two megaspores. The nucleus of the spore mother cell has not divided.

FIG. 121. Section through a single megaspore whose contour and large nucleus suggest that it is the direct product of a spore mother cell which has failed to divide.

FIGS. 122, 123. Older stages of megaspores.

FIG. 124. Median vertical section of tip of strobilus showing relation of sporangia to sporophylls and vascular system. The meristematic regions at the bases of the sporangium pedicels grow upward slightly by causing the megasporangia to appear sunken in the hollows thus formed. There were only megasporangia in this strobilus.

FIG. 125. Transverse section of strobilus through microsporangia. In the center of the figure is the axial strand surrounded by air chambers interspersed with meristematic tissue. At the right and left are two microsporangia, each showing the septum which incompletely separates it into two loculi. The rest of the diagram represents the cross sections of six sporophylls with their ligules.

FIG. 126. Apical portion of strobilus showing young sporophytes protruding from undetached megasporangia.

HULL BOTANICAL LABORATORY,
THE UNIVERSITY OF CHICAGO.

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX.

WILLIAM L. BRAY.

(WITH TWENTY-FOUR TEXT FIGURES)

[*Continued from p. 123.*]

THE GREAT PLAINS.

THIS great region is naturally divided into two sub-regions, (1) the prairie plains, from which, except for scattered remnants, the original Great plains deposits have been removed, and embraced in the central and east central provinces of Hill (*fig.* 1); and (2) the remaining areas of Great plains proper (Llano Estacado, Edwards plateau, and Stockton plateau).

The prairie plains.—This sub-region embraces the grass country of central and north Texas west of meridian 97.5°, an area over 50,000 square miles in extent. As previously stated, it is a vast region of denudation, presumably from a former plain which must have stood at a much higher level. Whatever may have been the overlying formations, the present stage of erosion presents exposures of various formations, each of which owes its individuality chiefly to the character of the strata now undergoing reduction. Taken as a whole the dominant vegetation is a grass formation, but upon the areas of sand and gravel exposure, and the hills, bluffs, and streamways, timber formations prevail. The provinces are the Grand prairie and those of the central denuded region; embracing (1) the granite country, (2) the Carboniferous area (Brownwood and Palo Pinto countries), (3) the upper cross timbers, (4) the red beds country, and (5) the Callahan divide.

THE GRAND PRAIRIE—Geologically this is a Lower Cretaceous area extending from the Colorado river (its eastern margin near Austin) northward beyond the Red river, its eastern boundary being the Black prairie or rich black land area of Texas. The western boundary of this province is a prominent and irregular escarpment overlooking the central denuded region, and the upper cross timbers at the north. The prairies, which are the dominant physiographic feature, are wide undulations interrupted by broad erosion valleys and occasional butte remnants of the former plain. The elevation of the province is from 800 to 1200 feet. The soil covering is but a thin veneering overlying alternating beds of chalky limestones and marls, which are very poor receivers or retainers of moisture. This condition suffices to offset the comparatively high annual rainfall (28 to 32 inches), so that this is a province of pronounced xerophytic grass formations, but still a transition from the mesophytic Austro-riparian to the xerophytic Lower Sonoran zone. In its temperature relations the province stands almost on the transition to the Upper Sonoran and Carolinian zones respectively, thus differing notably from the Rio Grande plain province which passes into semitropical.

Pure grass formations.— Ecologically the grass formations are strongly xerophytic and partake of the characters of the grass vegetation of the more westerly plains, though in a moderate degree. As already seen, the mean annual rainfall is sufficient, other things being equal, to give existence to semi-mesophytic formations. But the periods of brilliant sunshine and dry air which prevail, especially during the growing season, very quickly dry out the superficial covering of soil and drive vegetation into the resting stage. Under present conditions of pasturage the grass covering has been sadly reduced from its former occurrence. Formerly it was very compact and luxuriant. With the breaking up of this, moisture relations have changed, and the formation is now more xerophytic. Floristically it is impossible to say, with the meager data available, how the association of species compares with that of prairies and plateau plains westward, or to what extent the formation has changed under pasturage. It is certain from the general aspect of the formation, however, that the dominant species here are not dominant ones on the more western plains. In brief, the ecological type known as prairie grasses exists here, as distinguished from the high plains type.

The grass vegetation of the Grand prairie is accompanied by a very abundant vegetation of prairie annuals and herbaceous perennials, with lignescent, tuberous, or bulbous underground parts. These assist in giving the province individuality as a grass formation.

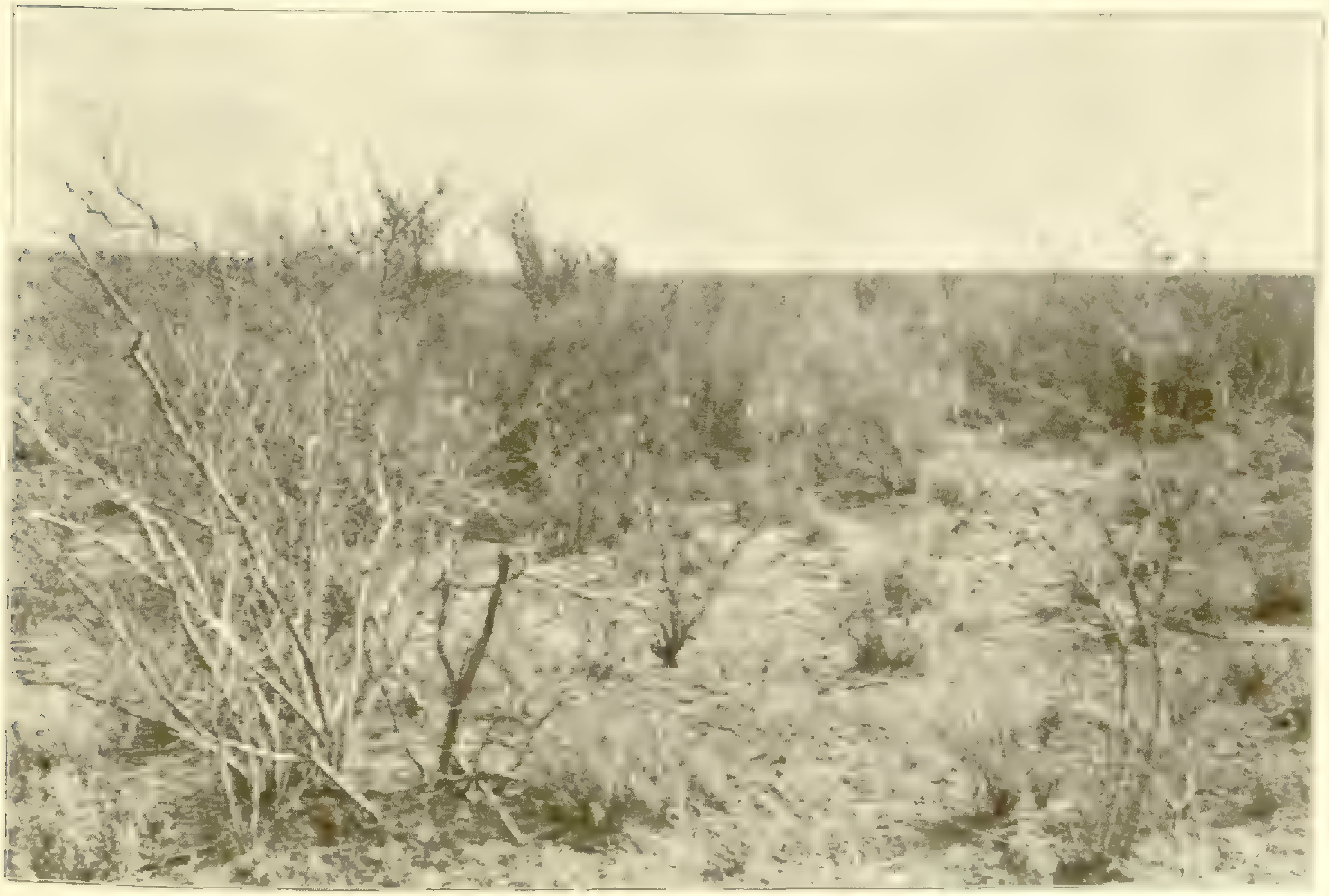

FIG. 7.—Rio Grande chaparral at Laredo: sage (Leucophyllum), "all thorn" (Koeberlinia), Mexican persimmon (*Diospyros Texanum*), and eight or ten other species.

Formations of prairie annuals.—Since the most conspicuous formations of this kind occur in other provinces, this type will be discussed later under a separate heading.

Chalk soil formation of herbaceous perennials.—The species associated in this formation number perhaps thirty-five or forty. It occurs throughout the province on the thinnest soils, but comes out especially on bare chalk slopes. Sometimes a single species prevails upon such places, but commonly there occurs a mixture embracing nearly all the species. Thus a careful collection upon a typical chalk area will yield more than three fourths of the species of the typical formation (*fig. 14*).

In all species the underground parts are reservoirs of food (and not infrequently of water) protected against the extremes of heat and drouth to which the arid soil is subjected. When the soil is wet by rains these subterranean organs quickly throw up vegetative organs, and perhaps flower and mature fruit before the brief period ends and they are again driven into the resting stage. The underground parts are of several types, as succulent fibrous roots with a thick zone of mucilaginous or saponaceous tissue (*Krameria secundiflora, Yucca rupicola*); woody subterranean tuberous caudex (*Liatris pycnostachya*); mucilaginous bulbs with impervious coats (Allium, Cooperia), and deep irregular or fusiform roots with hard flinty (sclerenchymatous) coat (*Asclepias decumbens*).

THE CENTRAL DENUDED REGION.—The granite and Carboniferous areas and the upper cross timbers together constitute a belt lying below the western escarpment of the Grand prairie, where the prairies are more or less interrupted by a more broken relief, which in part of the granite area becomes positively mountainous. This belt is marked on the more level areas by a surface covering or by deep beds of sand and gravel, where conditions favor the occurrence of an open timber formation and even a close forest covering in the upper cross timbers. Discussed from the standpoint of grass formation, the granite and Carboniferous areas (Burnet, Brownwood, and Palo Pinto countries of Hill, see *fig. 1*) are open-timber grass prairies, which with the spread of the mesquite (*Prosopis juliflora*) are losing their last remnants of pure grass formation.

The grass formation of this belt (the upper cross timbers not included) appears to have about the same character as that of the sand plains of the Rio Grande plain. The ecological conditions are very similar except as to temperature, and the results of this difference are apparent even superficially in the absence of certain semi-tropical species common at the south, and in the presence of Upper Sonoran or Carolinian species whose range extends into the middle northern states.

THE RED BEDS PROVINCE.—The vast level plains of reddish, chocolate soil make of this province one of the most unique features of the entire Texas region. This geological formation underlies the Staked plains, and has been exposed by the erosion of that area in the Pecos and Canadian river valleys. But the red beds plains lie between the Staked plains and the Grand prairie (more accurately the upper cross timbers), a width of 150 miles, and stretch away through Oklahoma and southern Kansas, a distance of 400 miles. Erosion and weathering have left wide, flat stretches of reddish landscape, either covered with fine, chocolate, silty sand, or exposing the bare rock. Violent bursts of rainfall wash away acres of prairie, often to the depth of several feet, carrying the chocolate flood silt to the coast country. Within the Texas region there are no large relief features in the red beds province, although the broad erosion valleys have to a certain extent the "Bad lands" aspect. The great extent of this province and its geographical position give it climatic relations which are apparent in the character of the vegetation.

As to atmospheric moisture, the stretch of 150 miles (the breadth of the province) from east to west means a variation in rainfall from 27 to 20 inches, and of evaporation capacity from 50 to 65 inches. The vegetation of the western part of the province has a more extreme xerophytic character than that of the eastern part. The northeastern parts sustain extensive mesophytic or semi-mesophytic culture formations with reasonable certainty. It is particularly a wheat belt. Toward the western border these formations become impossible except with seasons of higher rainfall.

As to temperature, while the entire province falls in the Lower Sonoran zone, its position as a whole far to the north of the Rio Grande plain gives it floristic relations more in common with the Upper Sonoran areas to the north. But within the province itself there exists this diversity, that the southwestern border receives much from the arid Sonoran flora of the southwest, at the northeast the incoming flora is a semi-mesophytic one from the northern prairies. This relation to the flora northward is promoted by the continuation of the red beds formation as far as southern Kansas.

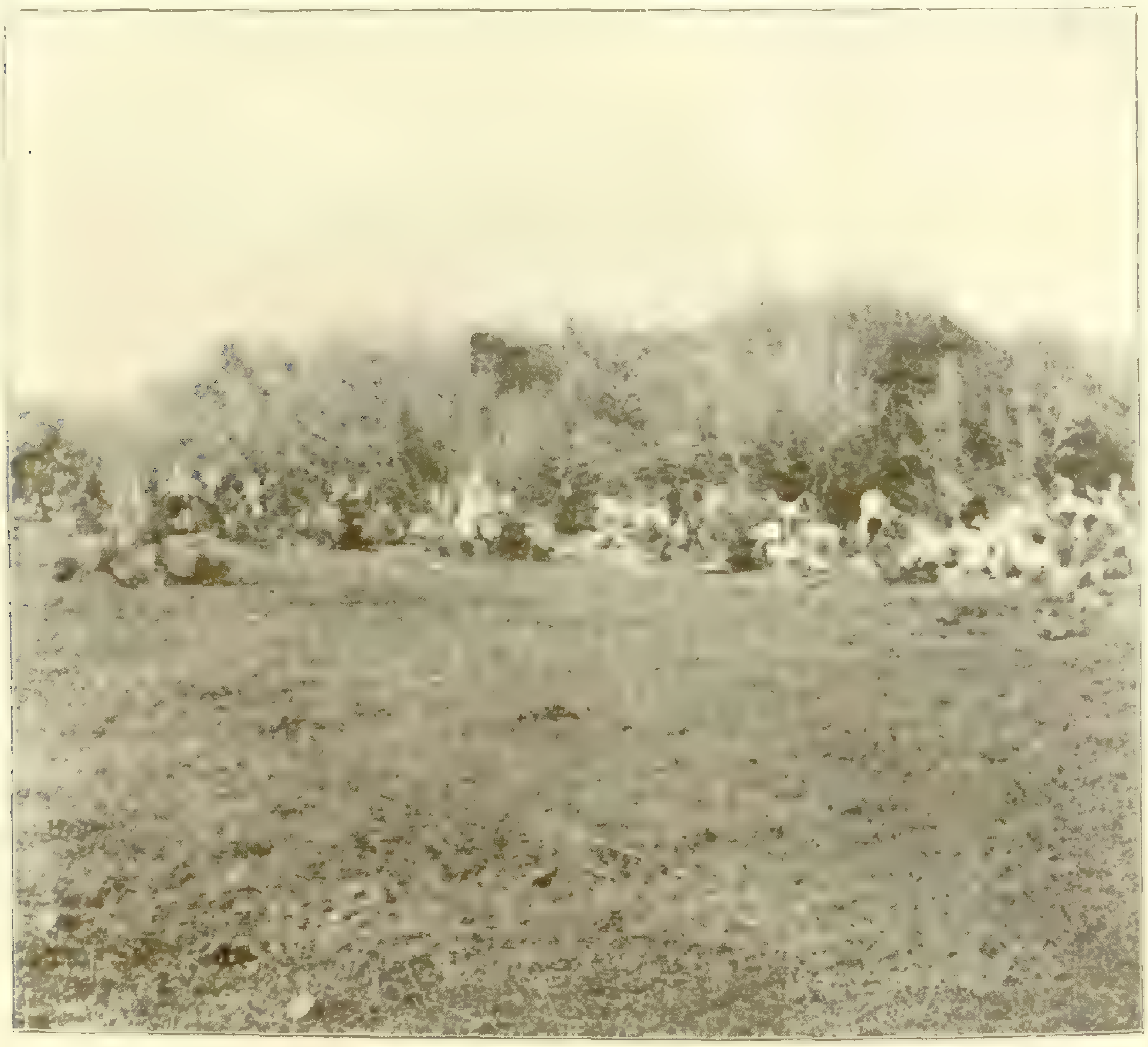

FIG. 8.—Edge of chaparral thicket, Port Lavaca.

The ecological conditions are most favorable for a pure grass plains formation. While it lies beyond the zone of chaparral formations, the mesquite already covers most of the western half of the province, undoubtedly modifying the structure and content of the grass formation. As to the general type of grass formation, the semi-arid climate makes of this a characteristic dry grass plains flora. Without a more specific study of this flora it will be impossible to show satisfactorily wherein lies its individuality as compared with the Grand prairie on the east and the Edwards plateau and the Staked plains on the south and west. It is probable that there is a real distinction, and that it lies chiefly in the peculiarities of the red beds formation. Two specific formations are constantly to be distinguished, (1) the *Hilaria Jamesii* formation, which occupies the lower stretches where sandy loam lies deeper, and appears like a vast field of heavy cultivated hay; and (2) the *Aristida fasciculata* formation, which occurs on ridges alternating with the lower areas of *Hilaria Jamesii*, and in its turn presents large tracts of waving grass fields.

Formations of prairie annuals.—It is not possible at present to say to what extent or wherein the prairie annual formations are distinct from those of other provinces. The soil conditions are such as to favor many species devoted to sandy soils. In the southern part of the province there are species from the south and southwest. At the north the prairie annual flora of Oklahoma and Kansas, in the same longitude, appears to be largely predominant. These formations prevail in such abundance in the case of some species as to form an important factor in the forage supply, especially in the early spring, when there is a solid mass formation. This disappears before the climax of the grass vegetation season (*fig. 17*).

The Great plains proper.—There are included in this region three provinces of the higher plains, namely Edwards plateau, the Staked plains, and the Stockton plateau (*fig. 1*).

THE EDWARDS PLATEAU.—This province forms the continuation of the Great plains east of the Pecos, from the southern limit of the Staked plains to the downfall at the Balcones escarpment overlooking the Rio Grande plain. The entire southern half between the Colorado and Devils rivers is marked by such deep erosion as to be mountainous. While a grazing country, this is not characteristically a grass plains, but a timbered area, and hence to be discussed especially under timber formations. But the grass vegetation even here contests for predominance, except on the most rugged hills.

The plains prairies.—To the northwest there is an area of the Edwards plateau which has not yet come to the stage of active and deep erosion, but is a typical open level plains country, with low relief lines of erosion remnants, and draws which lead into the cañons of the southern erosion area. This plains prairie is embraced approximately in the counties of Upton, Glasscock, Stirling, Concho, Crockett, Sutton, Schleicher, Tom Green, and Irion.

This Cretaceous area, both by its altitude and its westerly position, shares climatic conditions to a marked degree with the Stockton plateau and the Staked plains. As a result, the grass vegetation is of a more xerophytic character than in any of the provinces previously discussed. It is, in fact, almost fairly within the "short grass" country. Like the Grand prairie, this Cretaceous formation increases the xerophytic tendencies, so that here we find again a strong element in the perennial vegetation, which is more suffruticose than herbaceous, and made up of species with more xerophytic aspect and with affinities to the flora of the trans-Pecos provinces. But this element is in every way the counterpart of the chalk soil lignescent vegetation of the Grand prairie. In addition, the chaparral formations of the Stockton plateau and southwestward are encroaching upon this area.

THE STAKED PLAINS.—The Staked plains of the Texas region are simply a continuation southward of the Great plains area of western Nebraska, Kansas, and eastern Colorado, but cut off from the main area by the deeply eroded channels of the Canadian river on the north, and the Pecos on the west. To the north of the cañon of the Canadian river, Texas contains also a portion (the Pan Handle) of the main body of the plains. "This province is a vast constructional plain made up of flood débris from the mountains at whose base it lies. This mass of loose unconformable stuff is a monotonously flat plateau plain, whose only surface relief is the billowy swells and the shallow saucer-like depressions" (Hill). The open, porous, often sandy texture of the soil furnishes a favorable receiving area for rainfall. The soil water level is too far beneath the surface to be drawn upon even by deep-rooted trees. The vegetation is dependent, therefore, upon the immediate surface for its moisture, and alternates quickly between active growth and the dormant conditions according as the surface is moist or dry. But the porosity of the soil enables it to retain a larger percentage of precipitated moisture, so that the xerophytic conditions are not so extreme as the low rainfall (15 to 18 inches), the high altitude (3500 to 4000 feet), the high evaporation capacity of the air (60 to 70 inches), and its high velocity would lead us to expect. The Staked plains do not terminate at the south in an escarpment, but pass into the plains portion of the Edwards plateau by a broken series of outlying buttes and sand hills and plains. These sand plains not only form the transition from the Staked plains, but extend northward nearer their western side beyond the center of this province.

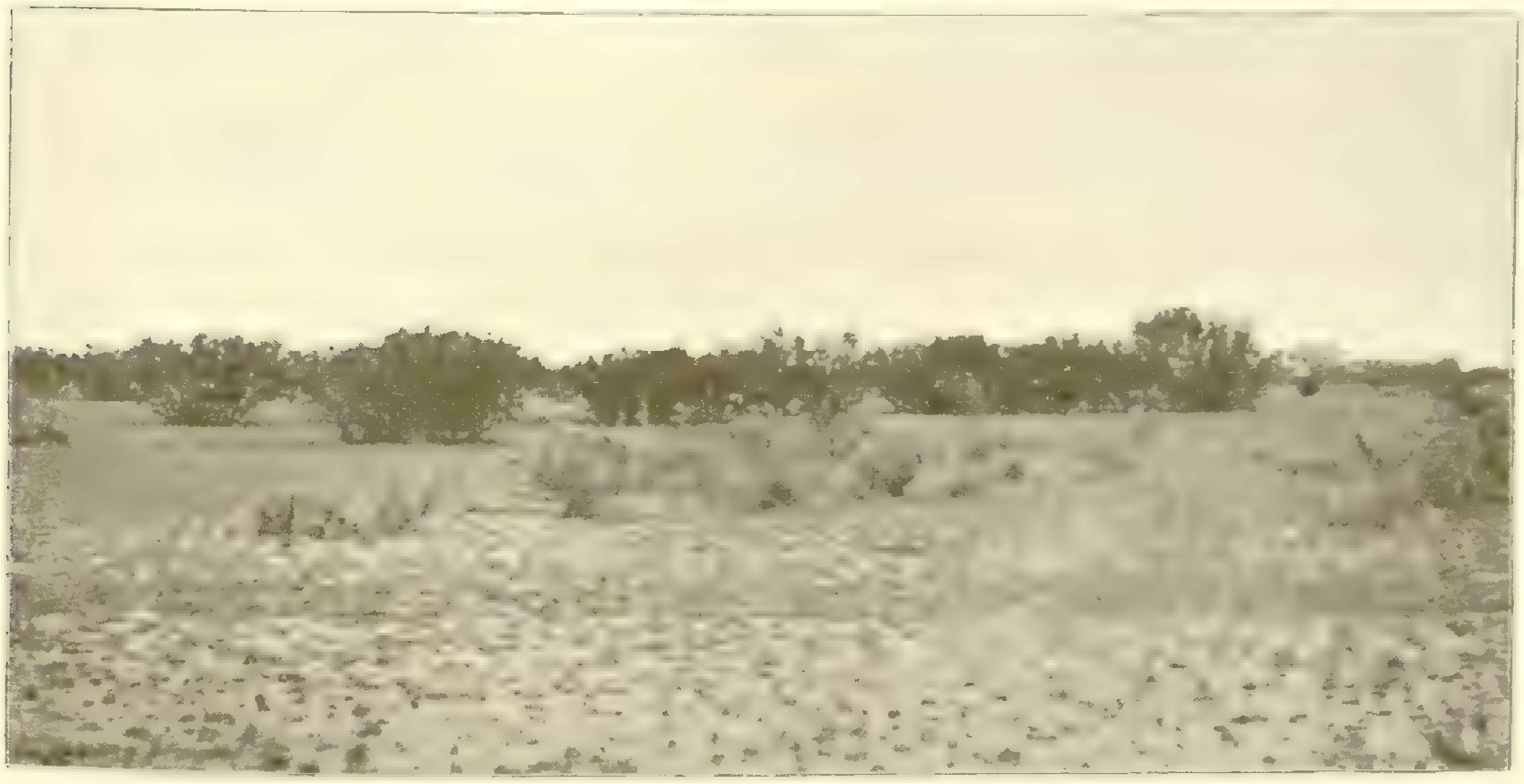

FIG. 9.—Characteristic occurrence of *Acacia amentacea* or black chaparral; on silty clay débris plain near Eagle Pass.

In its temperature relations the Staked plains is mainly Upper Sonoran. The transition from Lower Sonoran is made about the 3500 foot contour. Beginning at the southern limit of the plains, the Lower Sonoran vegetation, notably the chaparral formations, is represented in great strength. In going northward, ascending the plains, this vegetation becomes gradually more dilute, finally leaving a pure grass plain. The most apparent index of transition is furnished by the mesquite, which persists long after every other Lower Sonoran shrub has disappeared. Leaving a jungle of large mesquite below the escarpment, one comes upon a reduced growth upon the plains above, which becomes more and more dwarfed until at 3500 feet it is a mere clump of switches a foot tall, disappearing then absolutely. The same transition occurs in ascending the plains from the red beds province north of Red river, and where the Canadian cuts its cañon across the plains a Lower Sonoran flora has followed.

The grass formation of the summit plains is a solid grass floor of the short buffalo grass type. These grasses, in harmony with the sudden transition from moist to arid conditions, are adjusted to rapid changes from the dormant condition to luxuriant growth, and with the well-known characteristic that the growth already made when dry periods come on becomes perfectly cured as it stands, retaining all of the nutritious qualities which make these grasses economically valuable. All that remains alive during the dry periods are segments of the stem, which may be regarded as equivalent to buds or tubers or rhizomes. These are especially rich in carbohydrates. They are not underground nor connected with the soil by living parts, but merely anchored by the dead fibrous roots of the old growth. The cured grass serves naturally as a protective covering for the dormant living parts, although these are not often killed when the dry covering is burned off. Indeed, it is this quality of being able to endure fires that gives to these grasses the great advantage they possess in their constant struggle against woody vegetation (*fig. 23*).

The herbaceous species which accompany the grass vegetation are chiefly annuals. The lignescent rooted perennials so characteristic of the Cretaceous plains and prairies are mostly wanting, which is in harmony with the open porous soil texture. The very abundant *Yucca angustifolia* is an exception to this fairly constant condition. As to their affinity floristically, these annual species, while containing a considerable element common to Texas prairies south and southwest, are those which range over the whole stretch of plains to Nebraska and the northwest, thus indicating more positively the Upper Sonoran character of the province (*fig. 18*).

The true value of the zonal areas of the Staked plains is not strongly brought out, because the dominant grass vegetation is not so sensitive to temperature differences. Yet it seems pretty certain, though not yet established, that some of the very important species of grasses found in southern and trans-Pecos Texas and north Mexico do not extend upon the Staked plains, but that rather the floristic content of the formation agrees with that of the plains northward.

The grass formation is broken on the sand plains of this province because of the shifting character of the sands. This sand zone according to Dr. Havard, is entered upon going about twenty miles west of Odessa. "It extends thence south and east nearly to the Pecos and north to the very center of the plains. In this zone are the sand hills, a dreary chaotic belt of reddish sand, tossed by the wind into hillocks, cones, and ridges of various sizes and shapes."[7]

The lower belt of the sand zone marks the transition from Staked plains to the Cretaceous Edwards plateau. This is the only portion of the sand plains of which we have data as to the plant formation. Dr. Havard says of it: "The only grasses seen were a stout Andropogon (near *A. furcatus*) three to five feet high, with running roots holding the loose soil in their meshes; a Sporobolus (probably a form of *S. cryptandrus*), likewise erect and tall; and a large form of *Cenchrus myosuroides*." This indicates that the characteristic plains formation is entirely wanting. The herbaceous annuals are also those which prefer sandy soils. It appears from Dr. Havard's report that woody vegetation is the more dominant formation.

THE STOCKTON PLATEAU.—This is a subdivision of the

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[7] HAVARD, Contrib. U. S. Nat. Mus. **8**: (no. 29) 1885.

Edwards plateau, cut off by the cañon of the Pecos river. On the west the province adjoins the eastern front ranges of the mountains. Most of this area is a typical grass plain formation, of the general type found on the Staked plains and on the plains portion of the Edwards plateau. It will be seen that nearer the Rio Grande the surface is more broken, and that here woody vegetation predominates, also that the chaparral formation is encroaching even upon the level grass plains.

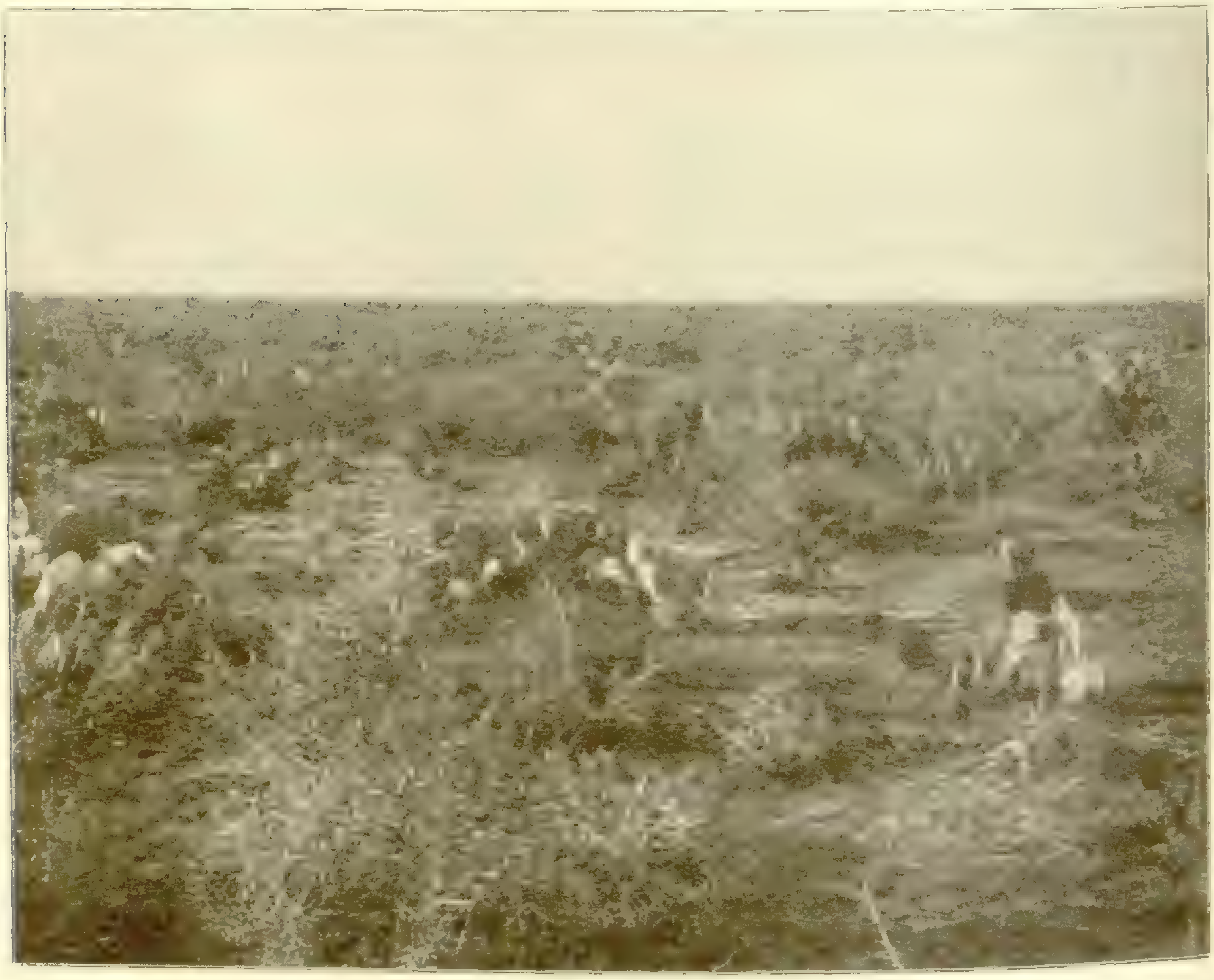

FIG. 10.—Chaparral formation at Corpus Christi; the growth shown is not so tall as that which covers the country generally in this region; the genera are chiefly Opuntia, Condalia, Zizyphus, and Celtis.

Compared with the Edwards plateau, this province as a whole is more elevated, and is in a zone of less rainfall and of greater evaporation capacity. It is more intimately a part of the arid plateau area of the Lower Sonoran zone, wich embraces north Mexico, southern New Mexico, and Arizona, and while it is only surmised that the grass formation would show this floristic relation, it is certain that other formations show it in a marked degree.

MOUNTAINS AND SOUTH PLATEAU SLOPE.

The Rocky mountains proper terminate before reaching the Texas region. The mountain axis continues southward, however, as an elevated plateau whose surface is much cut up by isolated mountain masses, some of which exceed 9000 feet in altitude. These masses are composed of Carboniferous limestone and sandstone, of Cretaceous limestone, and of igneous material. The high plateaus among them are mostly bolson basins filled with the débris of their bordering mountains. The soil conditions here and the moisture conditions growing out of these furnish the direct causes which operate to determine the distribution of plant formation in a region which possesses extreme xerophytic conditions independently of edaphic factors.

Viewed from the standpoint of the grass formation, this is a region possessing a grass floor climate in a surprising degree, for although the mountain masses are in some instances high and rugged, and covered with woody vegetation, the slopes of most of these up to 6000 and 7000 feet, the foothills, the wider plateau plains (for example, about Marfa and northwestward), and even portions of some of the desert bolsons, have a continuous grass formation. But in the mountains of the Great bend and their intervening bolsons (except in the Rosillos mountains, where good and available range grasses are found, according to Havard), on bolsons with loose wind-swept débris, and on arid gravelly mesas, there is only the most scattering bunch-grass formation, or even no permanent vegetation at all.

The bolson basins of this region, owing to the distribution of sedimentary filling, are lowest at the center and undrained. Consequently, the drainage water gathers at this place, in many cases accumulating in ponds or rather large lakes, and in all cases making alkaline flats of varying degrees of saltiness. The higher, less alkaline slopes of these bolsons are often covered with grama grass formation characteristic of the region. The alkaline flats, of course, possess a halophytic vegetation, of which salt grasses form a prominent part.

On the whole, the grass vegetation of the mountain and south plateau provinces falls under three types of formation: (1) the close grass floor formation; (2) the open bunch grass formation; and (3) the salt grass formation. Of these the third will be discussed under the special head of "halophytic formations."

The open bunch grass formation is floristically equivalent to the close grass floor formation. The open and bunched character of the formation is due to extreme dryness, and especially to the instability of the loose finer igneous débris, or the coarser gravelly or stony nature of the soils.

The close grass floor formation may be designated "grama grass formation," from the popular name of the one to several prevailing species. In this formation, the great majority of species making up the formations of the eastern provinces have been sifted out by increasingly arid conditions, and only those remain which mark the extreme limit of xerophytic adaptation in grasses. A summary of the adaptation features of this type of formation shows: (1) rapid transitions from active to dormant conditions; (2) great resistance to extreme dryness and heat (including fires) while in the dormant stage; (3) equally great recuperative power after extreme treatment, including apparent extermination from a given area; (4) large food storage of fats and sugars in portions which retain vitality during dormant periods, thus rendering quick growth possible; (5) the quality of perfect drying *in situ*, thus not only covering the soil and holding it in place, but also protecting the vital parts.

PURE FORMATIONS OF PRAIRIE ANNUALS IN THE PRAIRIE PLAINS.

In the preceding discussion of grass formations, the herbaceous annuals of the prairies have been treated simply as accessory elements in the formations, but of value in characterizing the formations differing somewhat in temperature and moisture conditions. But the annuals of the prairies in the west Texas region, as well as those in other parts of the Lower Sonoran zone, constitute a vegetation phenomenon which periodically overshadows everything else. This phenomenon is the annual wave of vegetative growth and floral display which sweeps over the prairies, temporarily submerging the grass vegetation itself. In the mutual adjustment of grasses and herbaceous annuals in this climate, the latter, mostly pure mesophytes, must take advantage not only of the returning rainy season but of the optimum period preceding the intense summer heat, and of the absence of competing grasses at that time of the year. It is a matter of record among cattle men that in the early spring, when grass forage is scarce, their herds often feed largely upon the

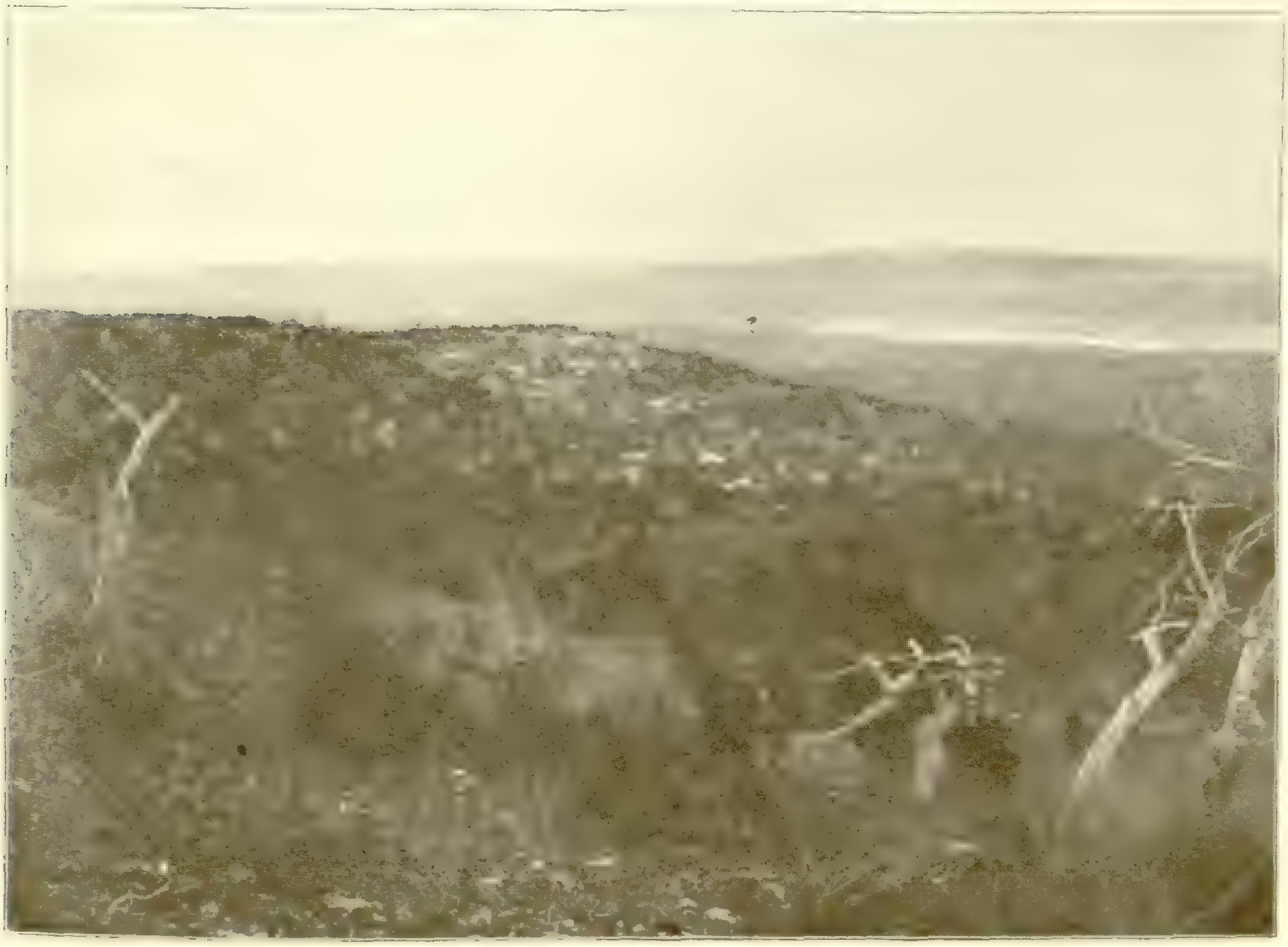

FIG. 11.—Hills covered with xerophytic timber, central mountainous region of Edwards plateau.

abundant young vegetation of these prairie annuals. Thus the "tallow weeds" (*Actinella linearifolia* and *Amblyolepis setigera*), which cover many miles of range, are much prized. Not only does this annual vegetation sweep as a wave over the prairie in the early spring, but the individual species mass themselves in pure formations of incredible compactness and extent (*fig.19*). Thus there may be successive waves of species. In harmony with the adaptation which leads to the massing of the species is the fact of the brilliance of floral display. This results in vast sheets of color. During the spring of 1900, which was unusually favorable for vegetation, the virgin prairie plains of Texas were literally a sea of color. In his survey of the Rio Grande plain during May, Vernon Bailey noted over twenty species which, as he expressed it, either occupied exclusively "acres of prairie" or "made miles of solid color." This was the case in the lower Rio Grande country (Corpus Christi to Brownsville) previous to May 10. The season of display ended about four weeks later on the northern boundary. At Austin by the first of July (often even two weeks earlier) a solid grass formation occupies the ground which had just previously been exclusively occupied by the "blue bonnet" (*Lupinus subcarnosus*). The continuity of grass formation seems in no wise disturbed by the periodical dominance of the annuals.

The species of these formations are of course dependent upon seed for their recurrence, and consequently are subject wholly to the caprice of rainfall during March and early April. When, as frequently happens, there is no rainfall of consequence during this period, the display of prairie annuals is very much reduced. Their adaptations are in the direction of seasonal adjustment rather than toward meeting xerophytic conditions.

II. WOODY VEGETATION.

Since the region under discussion includes only so much of Texas as is marked by a distinctly xerophytic vegetation, it follows that, except for river bottom and sheltered cañon timber, the woody vegetation is as a whole one of xerophytic aspect.

But it is of varying degrees of xerophytism according to its relation to the zones of decreasing moisture from east to west, that in the eastern provinces possessing some of the elements of the vast mesophytic forest of east Texas, while the extreme of xerophytism is reached in the desert bolsons of extreme west Texas. Recalling the common conception of the west Texas region as a grass country, it becomes a matter of surprise to learn how great is the proportion covered by woody formations, that is arborescent or shrubby vegetation in sufficient amount to form the chief covering.

This includes the following areas: the erosion area of the Edwards plateau; the hills, bluffs, and escarpment of the Grand prairie; the granite, Carboniferous, and upper cross timber areas; the higher mountain slopes and summits of the trans-Pecos mountains; the escarpment of the Staked plains and the Callahan divide; the chaparral of the Rio Grande plain, of trans-Pecos Texas, and of the lower Staked plains and adjacent Edwards plateau; the open streamways and the cañons; and finally many thousands of miles of mesquite-covered prairie. The energy and rate of encroachment of woody vegetation during the past half century lead one to believe that there is scarcely an area of consequence in the state that woody vegetation of some type will not occupy and cover more or less completely, granting of course that no artificial means are employed to check it.

The woody vegetation is here discussed under several types of formation, based largely upon moisture relations.

ARBORESCENT VEGETATION.

XEROPHYTIC FOREST FORMATIONS OF THE EROSION MOUNTAINOUS AREA OF THE EDWARDS PLATEAU (including the hill, bluff, and escarpment timber of the Grand prairie).—That portion of the Edwards plateau embraced between the Colorado and Devils rivers, and extending back 100 to 125 miles from the Balcones escarpment (southern downthrow of the Great plains) is very deeply cut by erosion channels, until the appearance is that of a mountainous country. Here are found in full operation those agencies which have worn so much of the surface elsewhere from a higher to an approximately level lower plane. The Cretaceous limestones, which on the grass plains portion of the Edwards plateau lie still unbroken, have here been cut through and exposed on all sides, thus not only offering lines of penetration for tree roots, but moisture facilities not available from an unbroken level surface. By this erosion, also have come about unequal conditions as between the summits and slopes of the hills, and the gorges and cañons between them. Certain Cretaceous formations, friable on exposure to weathering, outcrop on the hill slopes or summits, thus exposing an unstable foundation for vegetation. On these outcrops, often entirely bare, certain very hardy species can secure a foothold, and so anchor

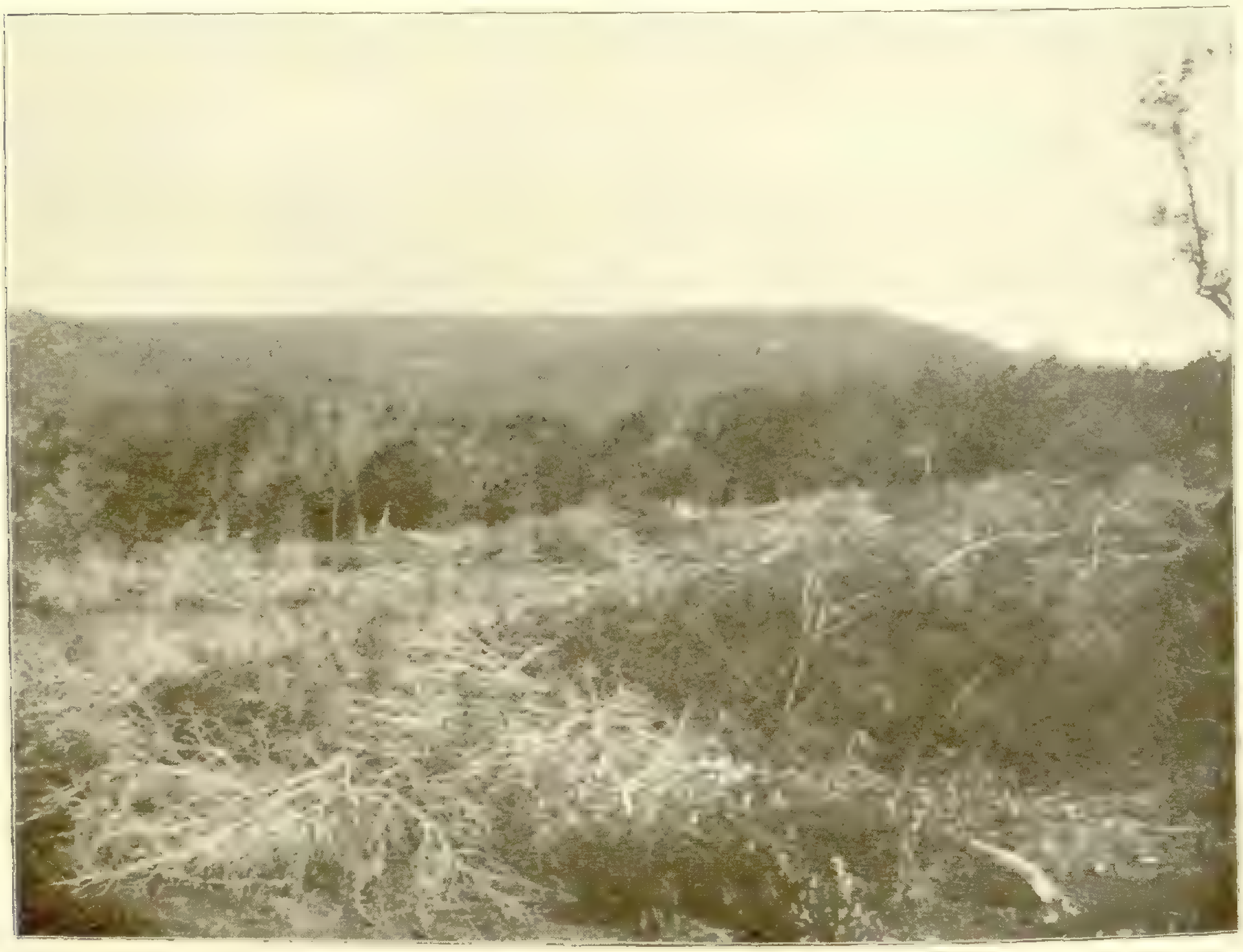

FIG. 12.—*Juniperus sabinioides* formation; a prominent feature in the xerophytic timber region of the Edwards plateau province.

this crumbling rock, even permitting a soil accumulation. The existence of similar conditions in the exposed formations in the Grand prairie results in carrying the timber vegetation over the hills and bluffs and bordering escarpments of this province far to the northward of the main body (*fig. 11*). This timber formation is an open stunted forest covering, which suffers extensive interruptions, but continues in spite of this to be the dominant vegetation feature of the areas just described. On some high arid divides it becomes reduced almost to shrubby dimensions.

Floristically, the chief elements of this vegetation are Lower Sonoran, of which many species range southwest into the Mexican mountains, or westward across the continent. In the western part of this province the presence of western mountain species is very marked. At the east there remains a strong element common to the Austro-riparian and Carolinian zones; but, aside from these indications of relationship, the province has a strong individuality. This is well shown by the fact that Austro-riparian and Carolinian species (when not present in the cañon timber) are vicariously represented by species stamped with the climatic characteristics of the region. Perhaps the most noteworthy case is that in which *Juniperus Virginiana* is succeeded by *Juniperus sabinoides*, the latter being a most characteristic xerophyte.

As to the content of the forest formation, this may vary from a pure formation of one species to a more or less uniform mixture of 50 or 60 per cent. of all the species. This variation is generally due to variations in soil condition. For example, a pure formation of *Juniperus sabinoides* may be due to an extensive exposure of very friable limestone like the Glenrose beds. In some cases the prevalence of a single species is due to the accident of its having gained the ground first. The following species formations are the most notable in this province:

Juniperus sabinoides formation.—This is the most important formation, partly because of its ecological relations, partly from its economic value. The formation is popularly called "cedar brake." Such brakes may be almost impenetrable over many square miles. The tree branches diffusely from the ground up, making a compact oval outline when standing free, and a dense interlacing of branches in close formation. Frequently at the ground the trunk itself divides into several approximately equal members. A pure formation of this juniper occurs characteristically where a friable limestone exposure lies almost bare of soil except a loose débris collected by the forest itself. Where such an outcrop occupies a slope whose angle is sufficient to make the friable rock surface unstable, an open cedar formation is the only woody vegetation present (*fig. 12*).

Aside from the very general use made of cedar in commercial ways, it occupies an important relation to moisture and soil conditions. Not only is the formation found to occupy areas where soil cannot accumulate except for the presence of this growth, but when cut or burned off it tends to reoccupy the ground most vigorously and to encroach upon the other species.

Quercus breviloba formation.—This is the so-called "mountain shin oak" of central Texas. On the summits of the high divides, where a thin soil is underlaid by unbroken limestone, the timber vegetation becomes very much dwarfed. In such cases the shin oak often becomes the dominant species and sometimes the only one, forming scrub thickets known as "shinneries." The mature plant may not exceed three or four feet in height. A familiar illustration of shin oak country occurs on the high divide between the San Gabriel and the Colorado rivers in Burnet county.

Quercus Virginiana formation.—This is in reality a dwarfed live oak formation which covers lower hill slopes or flats where the thin surface covering of black soil is strewn with coarse fragments of the broken underlying limestone. Such country, from its stony character is known as "hard scrabble," and the timber covering, often almost wholly of dwarfed live oak, is dwarfed and gnarled into a fitting counterpart of the ground structure (*fig. 13*).

ENCROACHMENT OF THE CRETACEOUS TIMBER FORMATION.—The forest covering of the erosion area tends not only to renew itself when removed, but it is a vigorous agressor upon previously open untimbered areas. This persistence may well be turned to account in any plans looking toward the maintenance of the forest covering on the more arid hills for prevention of soil erosion and destructive floods.

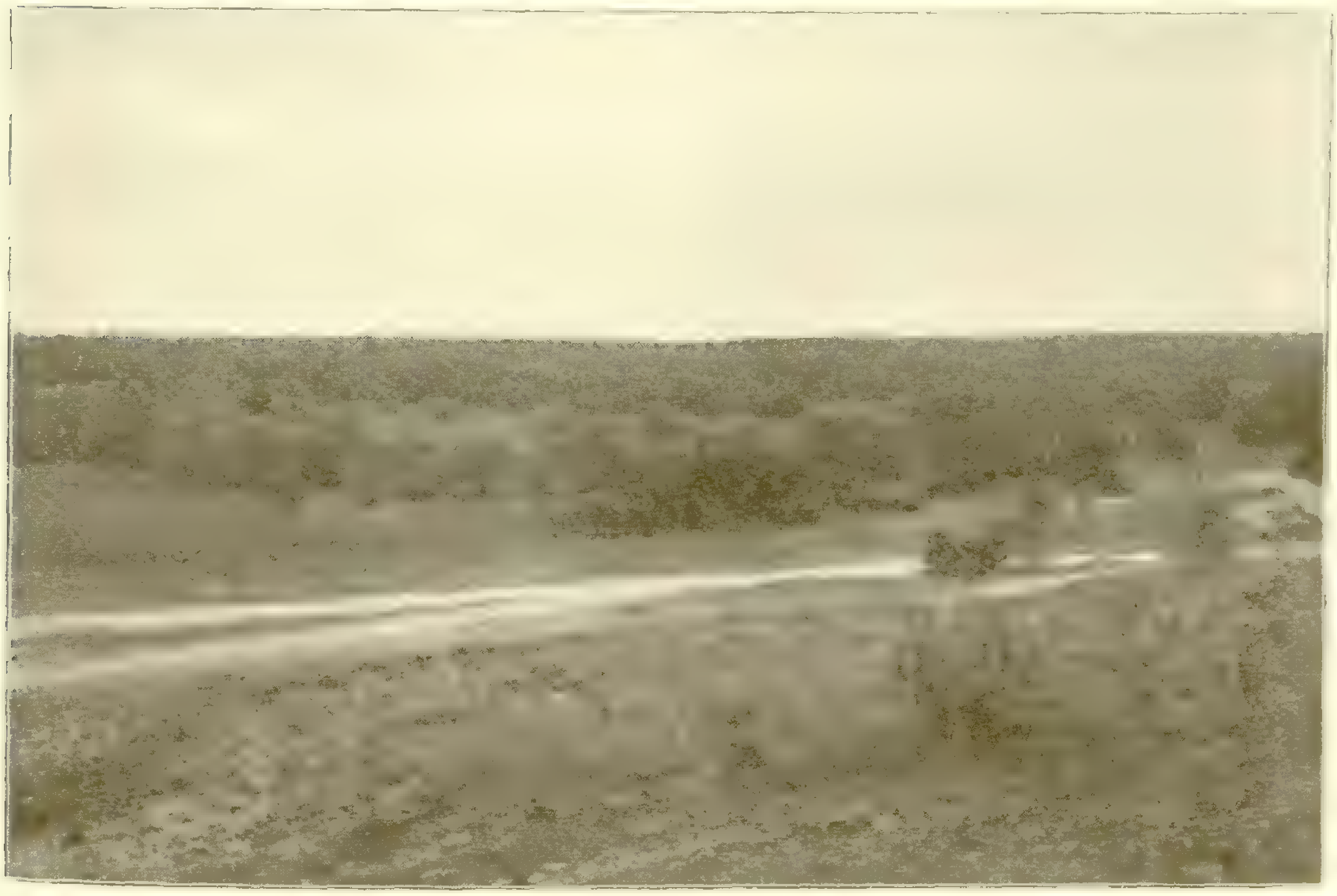

FIG. 13. — *Quercus Virginiana* (mountain form) formation; Cretaceous hills fifteen miles west of Austin.

XEROPHYTIC FOREST FORMATION OF THE MOUNTAIN SLOPES OF TRANS-PECOS TEXAS.—This formation is the counterpart of that just described for the erosion area of the Edwards plateau. It is a part of the forest covering of the arid mountain slopes of the southwest, including south Colorado, New Mexico, Arizona, and northern Mexico. Its area in Texas is practically limited to the upper slopes of the mountains in the great bend of the Rio Grande (above 6000 feet); to the dry upper cañons in these mountains; to the middle slopes of the Guadalupe and Davis mountains and their dry cañons.

The ecological conditions of these mountain slopes are more extreme than in the erosion area of central Texas, as shown in the following data. The annual rainfall is from 14 to 26 inches (approximate averages for each area respectively); the evaporation capacity is from 80 to 60 inches; the extremes of daily temperature in the trans-Pecos mountains is much greater than in the central region. Consequently the arborescent vegetation is one of more absolute adjustment to xerophytic conditions, and the semi-mesophytic species found in the central erosion area are either wholly excluded from the trans-Pecos area or relegated to the watered cañons. Of the arborescent species, *Pinus edulis*, *Juniperus pachyphloea*, *J. occidentalis*, *J. monosperma*, *Quercus grisea*, and *Q. Emoryi* are the principal ones. Not all of these are confined to the mountain slopes, for in watered cañons some of them form heavy timber of large size and good quality; but on the slopes their growth is dwarfed, the wood hard, the stems gnarled and misshapen, and they stand in a scant open formation.

The timber formation just described extends to certain physiographic features east of the Pecos river. These are the Staked plains escarpment, the remnant buttes of the Callahan divide (at least west of the 100th meridian), the sand hills of the southern Staked plains, and the cañon bluffs of the Devils and Nueces rivers. In the last instance, it is very dilute, being lost in the local formation, but in the other cases it is practically the only timber.

On the escarpment of the Staked plains, even as far as the northeastern border, there occur *Pinus edulis*, *Juniperus occidentalis* (in many straggling groves of small growth, according to Havard), and *Quercus grisea*. On the remnant buttes of the western half of central Texas there are close formations of a much dwarfed *Q. grisea*, in which this species attains a growth of only two to five feet, covering the ground in true chaparral fashion. Here also is found a very scattered formation of *Juniperus occidentalis*, which occupies also the lower mesas, becoming one of the chaparral species covering them.

On the sand hills of the lower Staked plains region one of the western mountain oaks (*Q. undulata* or *Q. Gambelii*) occurs in low thickets. To this region and the buttes and mesas eastward the trans-Pecos chaparral formation extends, and such reduced growths of *Quercus* and *Juniperus* as occur here become identified with the chaparral.

[*To be concluded.*]

UNIVERSITY OF TEXAS.

BRIEFER ARTICLES.

NOTES OF TRAVEL. VII.

A TROPICAL FOREST IN CERAM.

THE steamer Japara of the Netherlands India Packet Boat Company had a cargo of American pipe for a new oil well which was being sunk at Boela on the northeast coast of Ceram. To unload this pipe, the steamer anchored about noon on January 18 in the open roadstead, a half mile off shore. With our glasses Mr. Lathrop and I studied for some time one of those fascinating pictures of green and brown foliage which are the charm of steamboat travel in this tropical archipelago. We made up our minds that the low flat country and the hills behind it were covered with as rich a tropical forest as we had ever seen, but neither of us was prepared to find so many novel sights and interesting things as our short stay on land revealed.

Boela is a tiny clearing on the ocean edge of the forest, and not only has no harbor but its roadstead shoals so gradually that at low tide even a ship's boat grounds an eighth of a mile from the beach. So our party, the owners of the oil concession, the two travelers, and several native men and women, were forced to wade that distance before they reached the shore. The water was warm and our slight discomfort was quickly forgotten in the beauty or the oddity of countless things that attracted our attention.

As a first surprise, the beach was covered with thousands of moving shells of all sizes and shapes. These shells moved about in the most bewildering fashion. The rotting logs and even the mangrove bushes on the shore were literally alive with them. On examination each one was found to be the home of a hermit crab. Shells even smaller than the head of a shirt-stud were inhabited, and it was with difficulty that we found any uninhabited specimens. In our stay ashore we did not see a single hermit crab which had left its shell.

To add to this bewildering impression of moving strand shells, scores of small ash-colored fish were jumping about in the liveliest manner on the sand, often many yards from the water. These fish were so quick in their movements that it was many minutes before our boy succceded in capturing one with his hands. Although I did not observe any of these animals actually perched in the branches of the mangrove, I do not doubt the statement that they often climb low bushes near the strand, using their short ventral fins for feet.

Boela, the possible future oil city of the Orient, was decidedly in embryo. A few huts, made of the midribs of the sago palm and thatched with the matted leaflets of the same plant, were clustered about the landing shed and surrounded by young plantings of manihot, bananas, and a few papaya trees. At the end of the little village was a more or less comfortable bungalow in which lived an American mechanic from Pittsburg who had charge of the oil drilling machinery. Three of the most curious dogs I have ever seen greeted us as we walked up the path to the bungalow. They were crosses between the hairless Mexican dog and the "kampong" or native cur. These dogs were quite hairless except the tip of the tail, which was furnished with a brush of bright reddish-yellow hair, and the top of the head, which bristled with a stiff mop of the same color. The only cat of the place was one of the short-tailed breed which is common in this region.

As we strolled into the forest along a newly-made corduroy road, gorgeous butterflies flitted quickly or soared lazily across our path in such numbers that we were reminded of some of Alfred Russell Wallace's descriptions of his best collecting experiences in Malacca. Only twice before had we seen such quantities of these tropical insects, once on a small island in the gulf of Siam, and the last time on one of the pathways near Petropolis, Brazil. The newly fallen trees were swarming with insects and covered with fungi, and the log road was bright with red and yellow mushrooms of many different species. Every time we halted to examine a rotten stump or scratch away a few fallen leaves, swarms of black mosquitoes attacked us, and worried us with the suspicion that they were injecting malarial plasmodia into our blood.

The new oil well, which was soon reached, was surrounded by little pools of the dark brown liquid, and many tall forest trees about were killed by the crude oil which had flowed from the well before it was closed. The bubbling oil and gas was sputtering and hissing under the cap which had been screwed down to keep it in. Although inhabitants of Amboina who were interested in these wells expressed great hope of their success, as yet no large quantities of oil had been discovered. The roads which were being cut into the interior were expected to open up and determine the size of this new oil field. Near one of the oil wells stood giant forest trees, with bases buttressed by thin irregular plates which reached to a height of ten or twelve feet from the ground. On one of these trees, twisting about its gray trunk, was an epiphytic fern with dimorphic leaves, the basal ones like saucers closely appressed to the thick fleshy rootstock which they protected from the bright sunlight and its drying action.

On the same tree, while examining this fern, we disturbed a number of large gray ants which had built a paper-like nest on one of the broad flat buttresses. Like a company of veterans they rushed out of the nest and ranged themselves at regular distances from each other about their home. Every ant stood upright, curled its abdomen upward between its hind legs as if ready to sting, and with waving antennae awaited the enemy. On the parchment-like walls of the nest these warriors, as they hurried out, beat a sharp tattoo which was much louder but similar to that sounded by the termite warriors on the thin wooden walls of their galleries.

The newly made roadways through the forest were strewn with fruits which had fallen from the tops of the tall trees. Some of these were of the brightest orange and others a clear lemon-yellow, others still were purple and brilliant green. None, however, were edible, though many were most attractive looking.

In the tree-tops overhead, bright green parrots chattered, and a small cicada with a shrill but not unpleasant note kept up an incessant racket. Once a black parrot with red head flew low through the trees, looking like a flash of crimson light. Most of the birds, however, were in this season in the tops of the highest trees.

As in all tropical forests I have ever visited, the flowers in Boela were scarce. One bright crimson representative of the lily family, with a spike as large as a pineapple, was the only showy species observed. The botanical fancy is attracted in these forests by the curious creepers, which fling their supple stems about the tall forest trees and spread out their dark green tops above those of their supporting neighbors, until the latter are robbed of sunlight and slowly die. There are curious masses of stilt-like roots from which rise tall slender trunks; the pendant barbed tips of the rattan palm catch and hold you; delicate masses of green filmy ferns form soft pads on the fallen trunks; dusky chocolate-brown masses of the myxomycete (Stemonitis) color your fingers as you touch them; ugly looking incipient Polyporei exude oily looking drops of brown fluid; and the rotting bark contains a host of microscopic fungi. Epiphyllous algae and lichens are always abundant in these dark forests and are often mimicked by insects.

However little one may be interested in the insects of temperate regions, the constant buzzing of flies and wasps, and the fluttering of gorgeous butterflies in this virgin forest soon attract one, and leave a lasting impression of the activity of the animal world as compared with the world of plants. The ants alone, in their host of forms and curious habits, are sufficient to distract the most obstinate collector, and rob him of many hours he would have spent in adding new numbers to his herbarium. They are the most intelligent beings of the forest, and the solitary traveler finds a sort of intellectual companionship in watching their movements. The termites of the tropics are second only to the tree ants in interest. At Boela only the tree-inhabiting forms were found, and none of those curious kinds were seen which cultivate fungi in their nests. The dead stumps and trees were everywhere alive with them, and the decaying trees were rapidly removed by immense colonies of these wood-eaters. The virgin forests of the tropics would be well nigh impassible to collectors if the fallen branches and logs were not quickly riddled with the galleries of the white ants. They are above ground what the earthworm is below it. They reduce all dead wood to half-digested fragments.

This portion of Ceram is very sparsely settled, so sparsely, in fact, that during the whole time we spent at Boela we saw only two or three native Alfurians, who came off to the steamer in their small dug-out canoes to sell their large but coarse-grained bananas. They are a darker, more uncleanly race than the Javanese or Amboinese, and show traces of Papuan origin. Imported coolies from Java and Amboina are depended upon to work the drills at the oil wells.

But all idea of time was lost as we wandered through this forest, until the rapidly fading light (to say nothing of the rapidly devouring mosquitoes) gave warning that a hurried retreat must be made from this malaria-haunted shore. In the morning we saw Boela again, and it looked even more beautiful gilded by the rising sun than in the evening light. — DAVID G. FAIRCHILD, *Department of Agriculture, Washington, D. C.*

CURRENT LITERATURE.

BOOK REVIEWS.

The sea beach.

We fancy that there is a demand for a popular account of the seaweeds. It is not so important that the names and classification should be given, for such may be found in several well-written manuals and texts. What is probably most desired is a simple account of the life habits, and in part the life histories of such forms as are prominent in the tide pools, on rocky shores, in marshes, and in flats, and those that are washed up from the deeper waters after storms. A book by Augusta Foote Arnold[1] attempts to satisfy the thirst for seaside lore, and this review will discuss some points in her treatment of the marine algae. They are given only 50 pages in a book some 500 pages long, the remainder of the work dealing with the marine invertebrates, so it would be unjust to judge *The sea-beach at ebb tide* as a whole by the criticisms presented here.

It is hard to understand precisely the attitude of this author as regards the relation of popular science to technical science, or to put matters somewhat differently, the balance between the charm of natural history and the detail of a fully developed science. There is a little of both in this book, the science badly mutilated and sometimes incorrect, the natural history quite lacking the delicate fanciful touches that demand an imagination and yet must be tempered by many years of intimate contact with nature and by knowledge of scientific exactness and respect for it.

There is a brief account of the life habits, distribution, and uses of algae, and some statements about naming and classification which would lead the reader to suppose that especial emphasis would be laid upon these departments. And this is the case, for most of the space is devoted to the description and illustration of genera and species. These are apparently arranged after the system of a standard text, much abridged of course, the outline being presented at the beginning of each group. These synopses can be nothing but a mere dictionary-like table of names, for the account does not pretend to give the morphological characters of the groups. There are no keys, no microscopical examination is required, and for identification the reader (presumably beginner) must depend chiefly upon the figures. What then can be the value of this classification, out of sympathy with the purposes of morphology on the one hand and the spirit of natural history on the other?

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[1] Arnold, Augusta Foote: The sea-beach at ebb-tide. A guide to the study of the seaweeds and the lower animal life found between tide-marks. Small 8vo. pp. xii+490. *figs. 600+*. New York: The Century Co., 1901.

The illustrations are photographs of mounted algae on cards, and in some cases of preparations slightly magnified. While many are clear others seem to the writer quite valueless as a means of identification and unworthy of the book. Although the color of the specimen would help in this mechanical matching of mounts with figures, nevertheless there is sure to be much confusion. For example, how is *Enteromorpha clathrata* to be distinguished from certain Cladophoras? The figure of *Ectocarpus viridis* might do for several other species, the Callithamnia are quite impossible, and *Polysiphonia fastigiata* is certain to be confused with Sphacelaria.

One occasionally finds statements that lead to the belief that the author is quite untrained in natural history. Thus, on page 29 is the phrase "*Ectocarpus Hooperi*, a species of Ectocarpus first described by Mr. Hooper." This does not seem to be a fact, and the impression conveyed that naturalists name species after themselves is an implication of conceit far from being warranted by the conduct of these modest members of society.

The book has yet to be written that will tell the natural history of seaweeds with the charm of manner shown in the style of Miss Margaret Morley. And until such a treatment appears, it is much better that the amateur collector and observer of marine algae read Murray's *Introduction to the study of sea-weeds*, a simple and very interesting account, and one thoroughly grounded in science.— B. M. DAVIS.

NOTES FOR STUDENTS.

PROFESSOR ARNOLDI[2] has taken up the somewhat incomplete work of Shaw, and has made a careful study of the development of the endosperm of *Sequoia sempervirens*. Free nuclear division takes place in the usual manner in an evenly distributed peripheral layer of protoplasm, but very soon there is a denser accumulation of protoplasm at the lower end of the sac. When the formation of walls begins, three regions of the endosperm may be distinguished, the upper, the lower, and the middle. The upper, and particularly the lower, develop faster than the middle, so that the ends of the sac become filled with a solid tissue while the nuclei are still almost free in the middle portion. Each nucleus of the middle portion now becomes surrounded by a wall which is open on the inner side: the walls grow inward and when the center is reached, walls are formed at the inner ends of the cells. The nucleus now begins to divide, and each of these cells ("alveoli") becomes divided into several cells. Archegonia are formed only from these alveolar cells of the middle region. At the time of fertilization, the upper and lower portions of the endosperm consist of small-celled tissue, while the middle portion is alveolar. Sequoia is regarded as a connecting link between Gnetum and the angiosperms on the one hand and between gymnosperms and the archegoniates on the other.

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[2] ARNOLDI, W.: Beiträge zur Morphologie einiger Gymnospermen. I. Die Entwickelung des Endosperms bei *Sequoia sempervirens*. Bull. des Natur. de Moscow. Pp. 1–13. *Pls.* 7–8. 1899.

In a later paper[3] he has described the archegonia and pollen tubes of the same species. The archegonia are very large, and some sections show as many as sixty. They sometimes occur singly, but are often grouped. In development they resemble the archegonia of the Cupressineae, since they are often in direct contact with each other and do not form any ventral canal cell. There are no proteid vacuoles. The neck consists of two cells, in this respect resembling the older gymnosperms.

The pollen tube grows through the nucellus, not between the nucellus and integument, as described by Shaw. At the time of fertilization the pollen tube contains the two male cells of equal size, and two small nuclei, one of which is the tube nucleus and the other "the nucleus of the cell which united the generative cell with the microspore wall." The general structure of the pollen tube and its contents agrees with the Cupressineae. The morphological considerations, together with the geographical distribution, lead to the conclusion that Sequoia is nearly related to the ancient type from which the modern Araucarias and Cupressineae have descended.—CHARLES J. CHAMBERLAIN.

CONNECTING THREADS which establish protoplasmic continuity between adjacent cells have been studied by Mr. Hill[4] in the embryo and seedlings of *Pinus pinea* and in the mature tissues of *P. silvestris*. Some attention was also paid to the endosperm of *P. pinea*. The endosperm consists chiefly of rather large rounded cells, but a close examination shows that in many cases an internal division has occurred. The threads are evenly distributed in the young walls, but are grouped in the older walls. Near the cotyledons the cells are smaller, the threads thicker, and there are traces of ferment action. Ferments from the cotyledon pass into the endosperm through the threads, and by the same route food materials pass from the endosperm to the embryo.

In the seedling the absorptive side of the cotyledon is more abundantly supplied with threads than the side not exposed to the endosperm. There are no threads in the external walls of the epidermis, and but very few connecting the guard cells with their neighbors.

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[3] ARNOLDI, W.: Beiträge zur Morphologie und Entwickelungsgeschichte einiger Gymnospermen. II. Ueber die Corpuscula und Pollenschläuche bei *Sequoia sempervirens*. Bull. des Natur. de Moscow. Pp. 1–8. *Pls. 10–11.* 1899.

[4] HILL, A. W.: The distribution and character of connecting threads in the tissues of *Pinus silvestris* and other allied species. Phil. Trans. Roy. Soc. London B. **194**: 83–125. *pls. 31–35.* 1901.

All parenchyma cells show a general resemblance in the character of their threads, the threads on the end walls being irregularly scattered, while on the side walls they are grouped. In the phloem all the sieve tube threads show a characteristic median dot. The albuminous cells at the edge of the phloem of the leaf have their threads grouped in localized thickenings on the walls, and serve to pass materials from the mesophyll to the phloem. The very numerous threads of the root cap form a connection with the free surface of the root and with the periblem.

In the mature tissue of *P. silvestris* the threads in the cortical tissue are similar to those of the seedling. In the phloem there is no connection between the sieve tubes and the bast parenchyma or the starch medullary ray cells. The sieve tube threads on the radial walls have a median dot. The torus of the bordered pit is probably traversed by threads which soon disappear. In the leaf, the distribution is about the same as in the cotyledon. The endodermis, with very numerous threads, is in close connection with the cortex and the stele. In the pericycle, living cells are connected by threads, but there is no connection between the pericycle and the lignified transfusion tissue.

In general, the main direction of threads in the cortex and phloem is tangential. The transitory nature of certain threads explains the absence of threads between the sieve tubes and medullary ray cells. Except in the medullary rays and in the cork cambium, the threads are chiefly on the radial walls. This suggests that in conifers food supplies and stimuli are conducted mostly in a tangential and vertical direction.—CHARLES J. CHAMBERLAIN.

OPEN LETTERS.

A CORRECTION.

In the June number of the Botanical Gazette (31:441) there was published by Ernst A. Bessey, of the U. S. Department of Agriculture, a review of *Bulletin* 49 of the Oklahoma Agricultural Experiment Station entitled *A rhizomorphic root-rot of fruit trees*. The reviewer made the statement that "This has been shown by von Schrenk and others to be caused, in all probability, by a hitherto unidentified rhizomorph-producing fungus." The reviewer having failed, on request, to cite references to these publications of "von Schrenk and others" in support of his statements, and having thought it "inadvisable" to correct the same when asked to do so, the following brief statements are submitted for the information of those interested.

November 6, 1889, von Schrenk identified the fungus in question as "one of the most dangerous tree fungi known, *Agaricus melleus*." (Letter to Horticulturist of the Okl. Agr. Exp. Sta.) Some more of the same material was submitted to Dr. B. T. Galloway, and under date of November 10, 1899, Dr. Galloway stated that "the fungus is the edible mushroom, *Armillaria mellea*." (Letter to Horticulturist Okla. Agr. Exp. Sta.) In the *Orange Judd Farmer* for January 12, 1901, von Schrenk says, "I suspect that possibly the fungus when determined will prove to be the same as a fungus very common in both Europe and America, the *Agaricus melleus*, or honey mushroom." This last statement is quoted in the *Bulletin* of this Station above referred to.

These statements will show clearly the state of the investigations of "von Schrenk and others" at the time stated. Perhaps in the future we shall have from these sources some valuable publications regarding this subject, but at present none such exists to my knowledge. It is hoped the above explanations will clear away some misconceptions and prevent the inference that this disease had already been investigated by members of the staff of the Department of Agriculture.

E. Mead Wilcox.

Oklahoma Agr. Exp. Sta.,
Stillwater.

NEWS.

AT THE recent Denver meeting of the A. A. A. S. Dr. D. T. MacDougal was elected general secretary for the ensuing year.

THE University of Glasgow, at its ninth jubilee, celebrated in June last, conferred the degree LL.D. upon Professor W. G. Farlow, of Harvard University.

PROFESSOR F. O. BOWER of the University of Glasgow is one of three representatives appointed to attend the bicentennial celebrations of Yale University next October.

THE University of Chicago at its last Convocation conferred upon Mr. A. A. Lawson and Miss Florence May Lyon the degree Ph.D. Miss Lyon has been appointed associate in botany and Head of Beecher Hall in the University of Chicago.

M. EUGENE AUTRAN has severed his connection with the Boissier herbarium at Geneva, Switzerland, and has been appointed botanist to the botanical garden of Buenos Ayres. He is also a member of the staff of the botanical section of the Argentine Department of Agriculture.

THE FOLLOWING RESOLUTION was adopted by section G of the A. A. A. S. at the recent Denver meeting:

Resolved: That it is the sense of this section that it would be advisable to establish a research laboratory in connection with the proposed agricultural experiment station in Porto Rico by the Department of Agriculture. Such a laboratory would offer most valuable opportunities for the prosecution of investigations in nearly all branches of botanical science, and would do much to supplement the facilities already offered by American institutions. Extended economic experiments in the tropics must rest more or less directly upon purely botanical research, and the establishment of such a laboratory would do much to strengthen the efficiency of the experiment station. This resolution is not to be taken to mean that the research station should be placed in the same building or buildings with the experiment station, but should be located at the point most favorable for the work in question.

DR. CHARLES MOHR, the venerable botanist, for many years a resident of Mobile, Alabama, died at his home at Asheville, N. C., on July 17. Dr. Mohr was for some years a special agent of the Forestry Division of the U. S. Department of Agriculture, for which he prepared a monograph on *The timber pines of the southern United States*, published in 1896. His most recent work is *Plant life of Alabama*, the result of exploration and study of the flora for forty years. This volume, which has been nearly three years in the government press, was issued on July 31, unhappily too late for the author to see the full fruition of his labors. This work we shall review later. We learn from *Science* that he had in preparation a volume on the economic botany of Alabama, which is probably too incomplete for publication. He published some years ago a pamphlet on the *Botanical resources of Alabama*.

THE FOLLOWING PAPERS were read before the Botanical Society of America at the recent Denver meeting: J. C. ARTHUR, Clues to relationship among heteroecious plant rusts; W. J. BEAL, Some of the changes now taking place in a forest of oak openings; C. E. BESSEY, Early winter colors of plant formations upon the great plains; E. G. BRITTON and A. TAYLOR, The life history of *Vittaria lineata;* F. E. CLEMENTS, The fundamental phenomena of vegetation, The plant formations of the Rocky mountains (with lantern slides), and A system of nomenclature for phytogeography; W. A. MURRILL (by invitation), The anatomy of the embryo and seedling of *Tsuga Canadensis;* B. L. ROBINSON (address of retiring president), Problems and possibilities of systematic botany; WM. TRELEASE, A suggested hybrid origin of *Yucca gloriosa* (with lantern slides).

The officers elected for the ensuing year are J. C. ARTHUR, *president;* B. T. GALLOWAY, *vice president;* D. T. MACDOUGAL, *secretary;* A. HOLLICK, *treasurer;* C. E. BESSEY and WM. TRELEASE, *councilors.*

THE FOLLOWING PAPERS were read before section G of the A. A. A. S. at the recent Denver meeting: W. J. BEAL, Lantern views of the Botanical garden at the Agricultural college of Michigan; C. E. BESSEY, The morphology of the pine cone; ALICE EASTWOOD, General botanical features of the Coast mountains of California; B. D. HALSTED, Notes upon colors of salsify hybrids; A. C. LEWIS, Contribution to the knowledge of the physiology of karyokinesis; D. T. MACDOUGAL, Thermal relations of plants, and Comparative climate of a meadow and a hemlock forest; AVEN NELSON, Some aspects of the Wyoming desert flora; L. H. PAMMEL, The xerophytic vegetation of the Uintah mountains; F. RAMALEY, Observations on *Egregia Menziesii,* and the plants of the eastern foothills (with lantern slides); A. D. SELBY, Experiments with lime and solutions of formaldehyde in the prevention of onion smut, and germination of seeds of some common cultivated plants after prolonged immersion in liquid air; E. E. SLOSSON, Effect of salt solutions on seeds and plants; WM. TRELEASE, Some protective leaf movements induced by winter temperature (with lantern slides); L. M. UNDERWOOD, The location of a tropical research station in Porto Rico; V. S. WHITE, The Tylostomaceae of North America.

The officers elected for the ensuing year are D. H. CAMPBELL, *vice president;* and H. VON SCHRENK, *secretary.*

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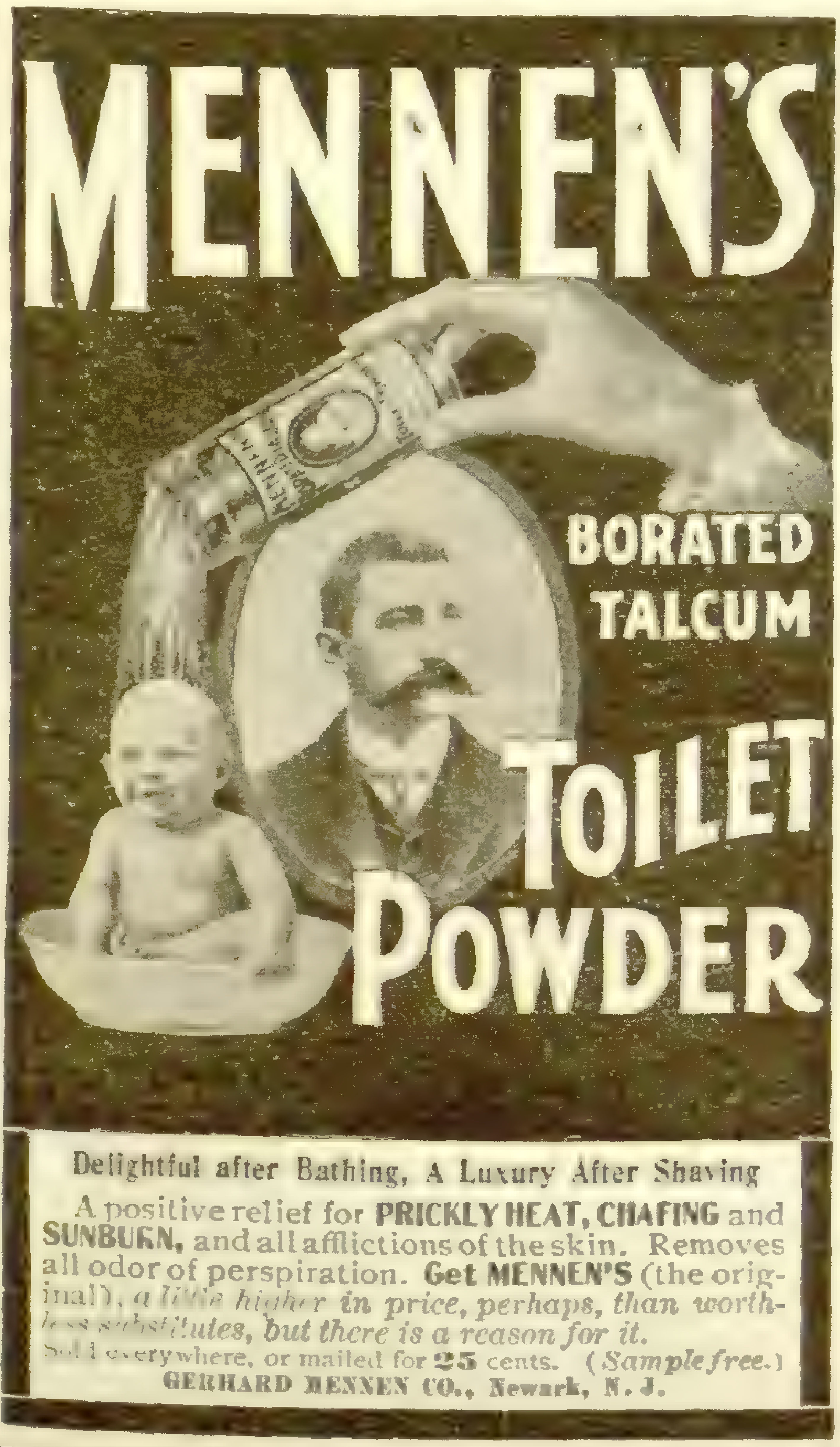

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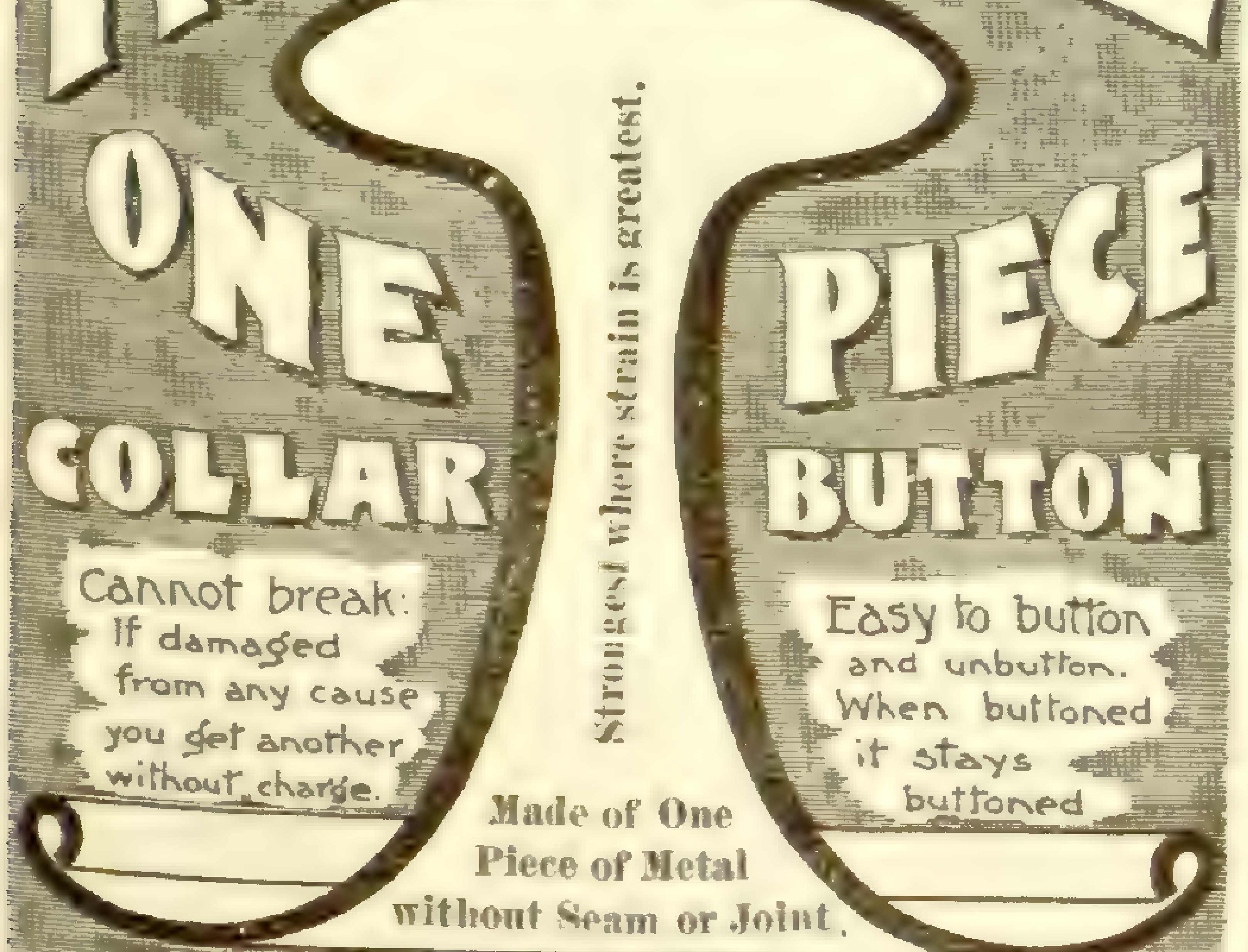
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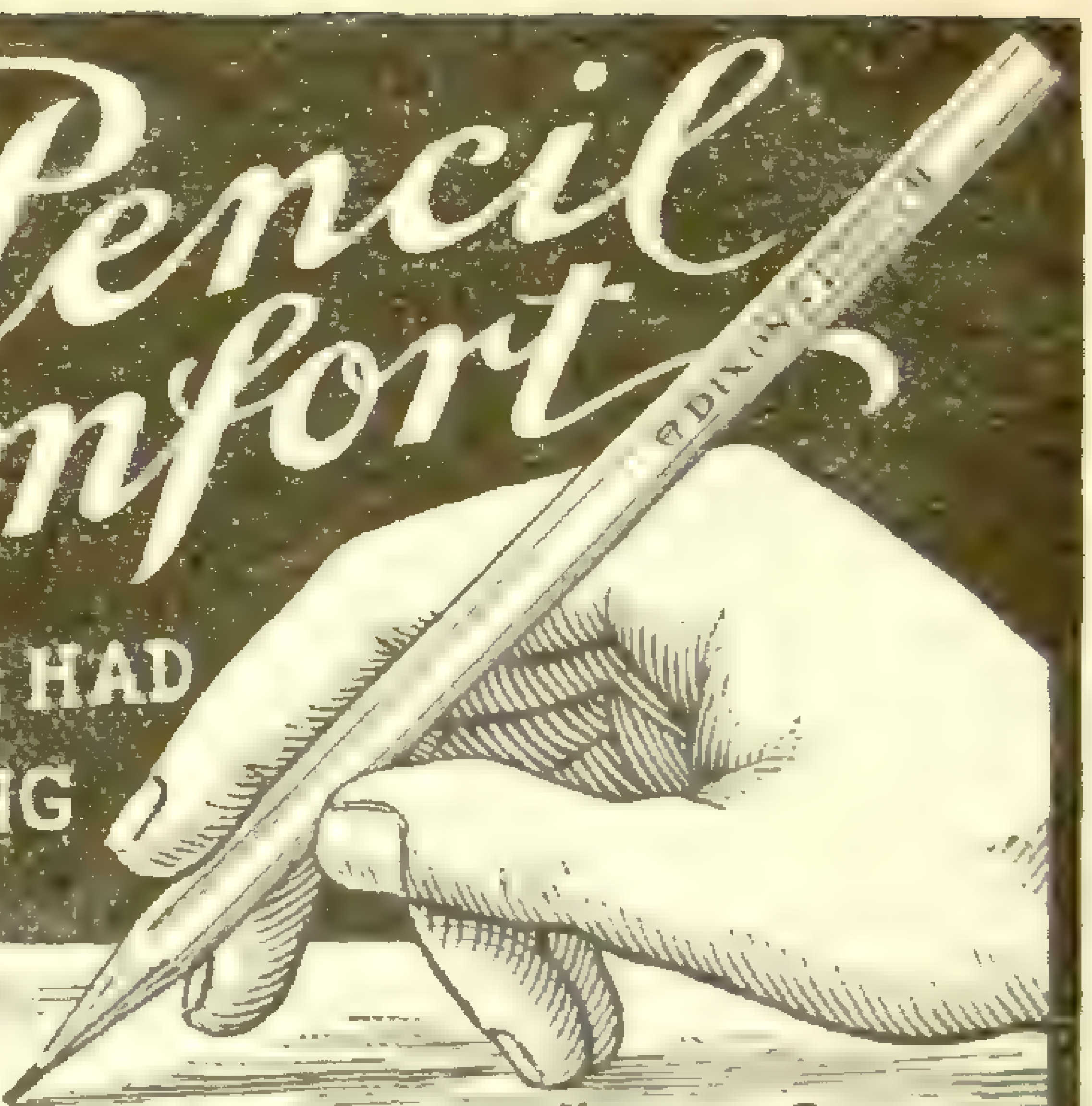

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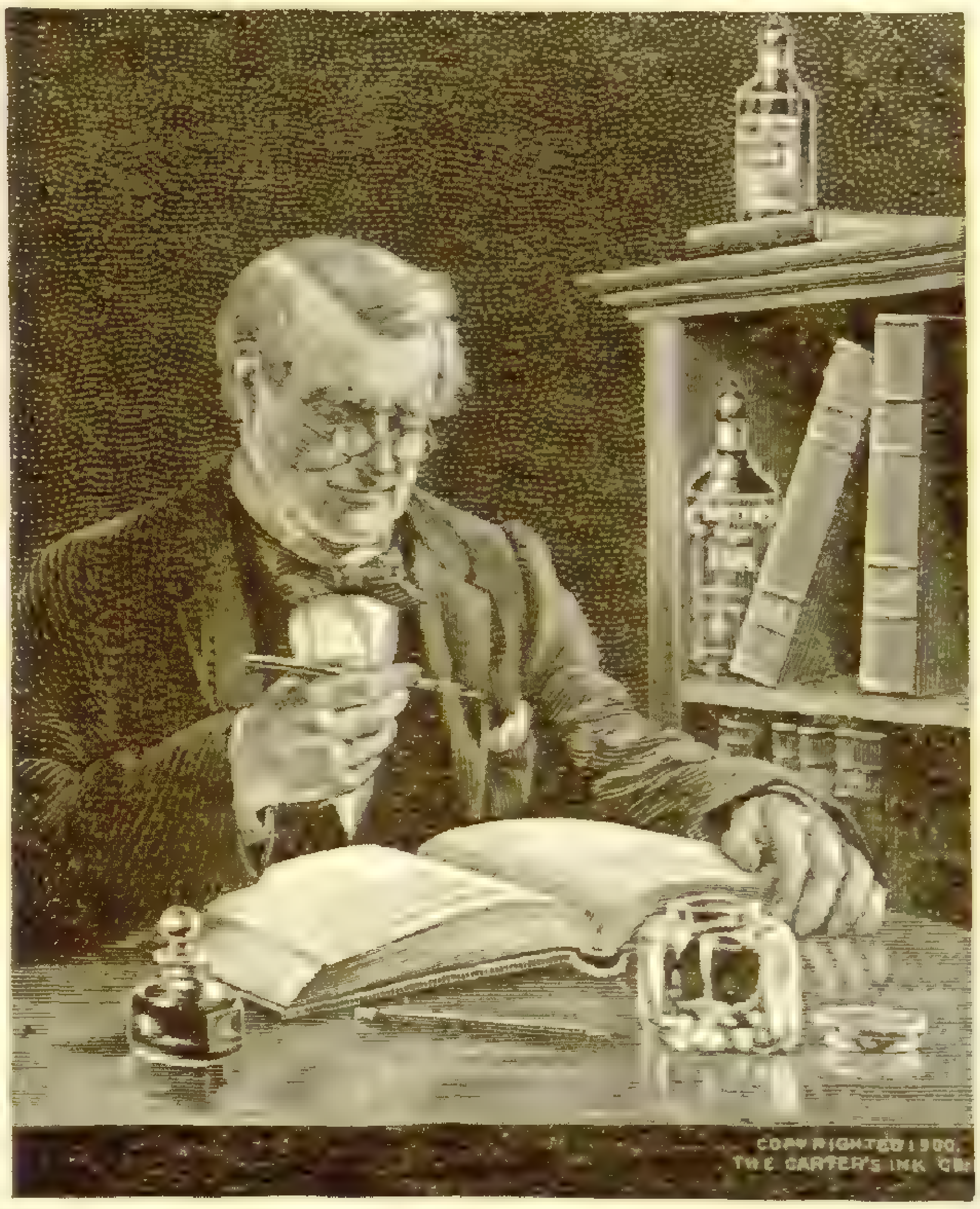

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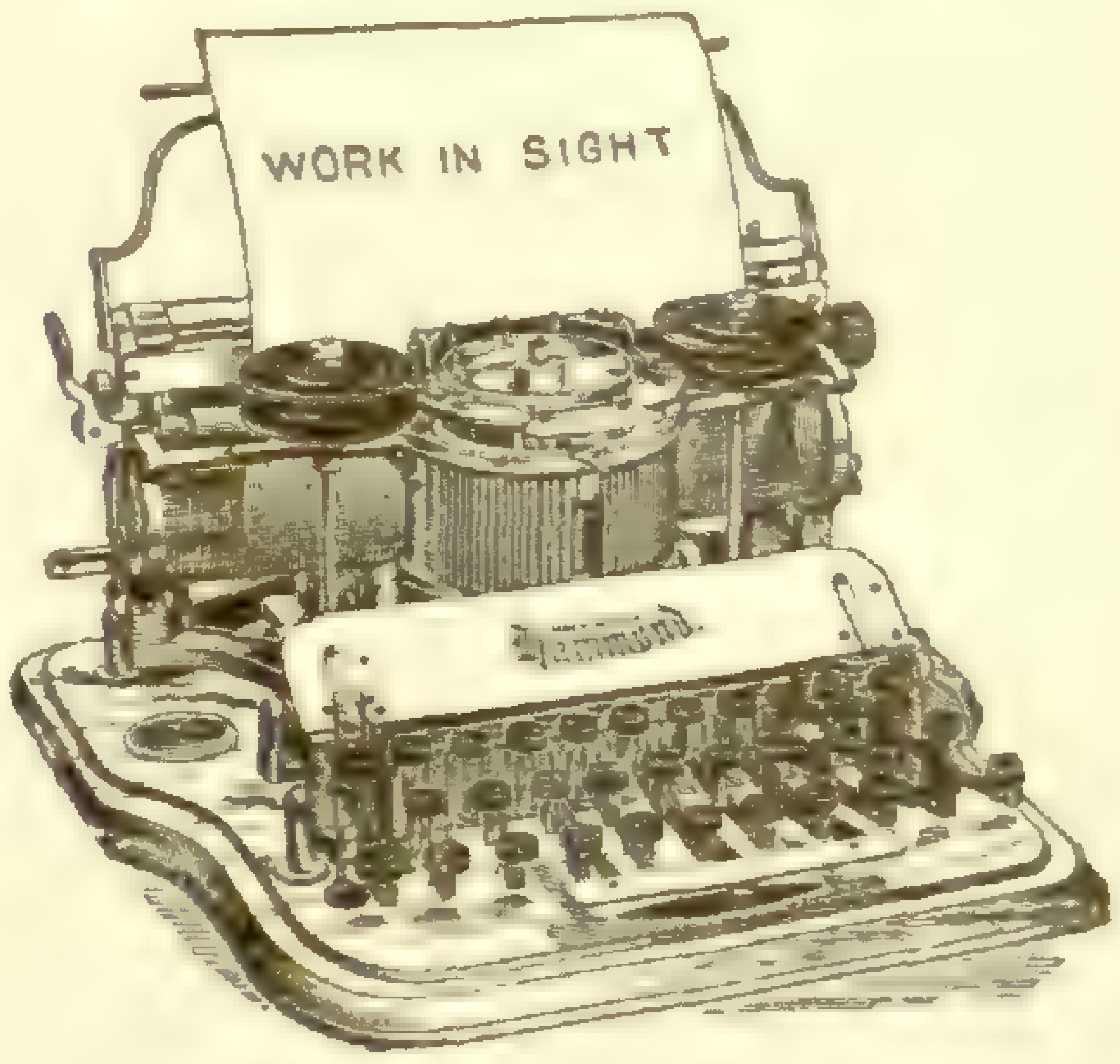

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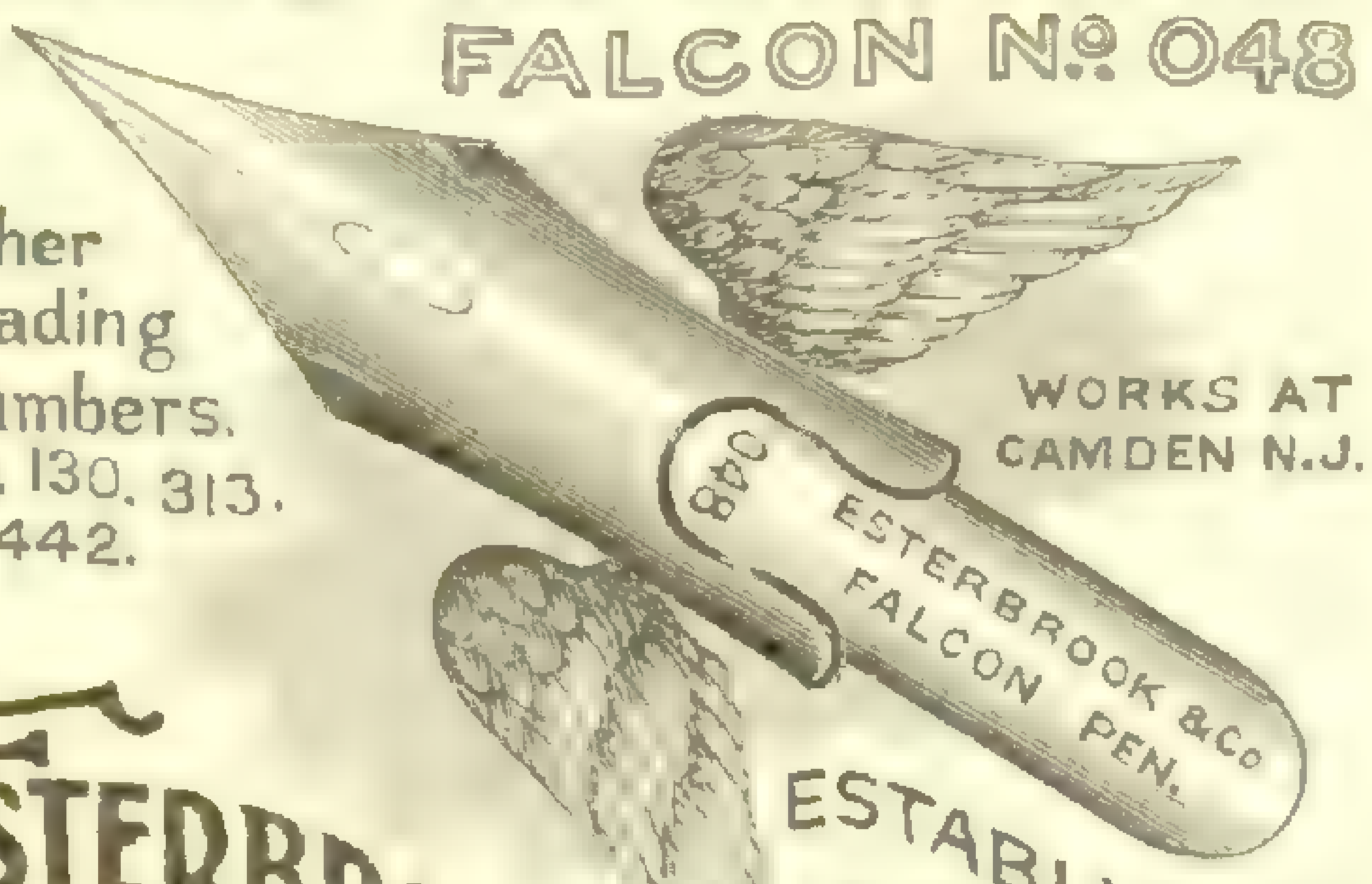

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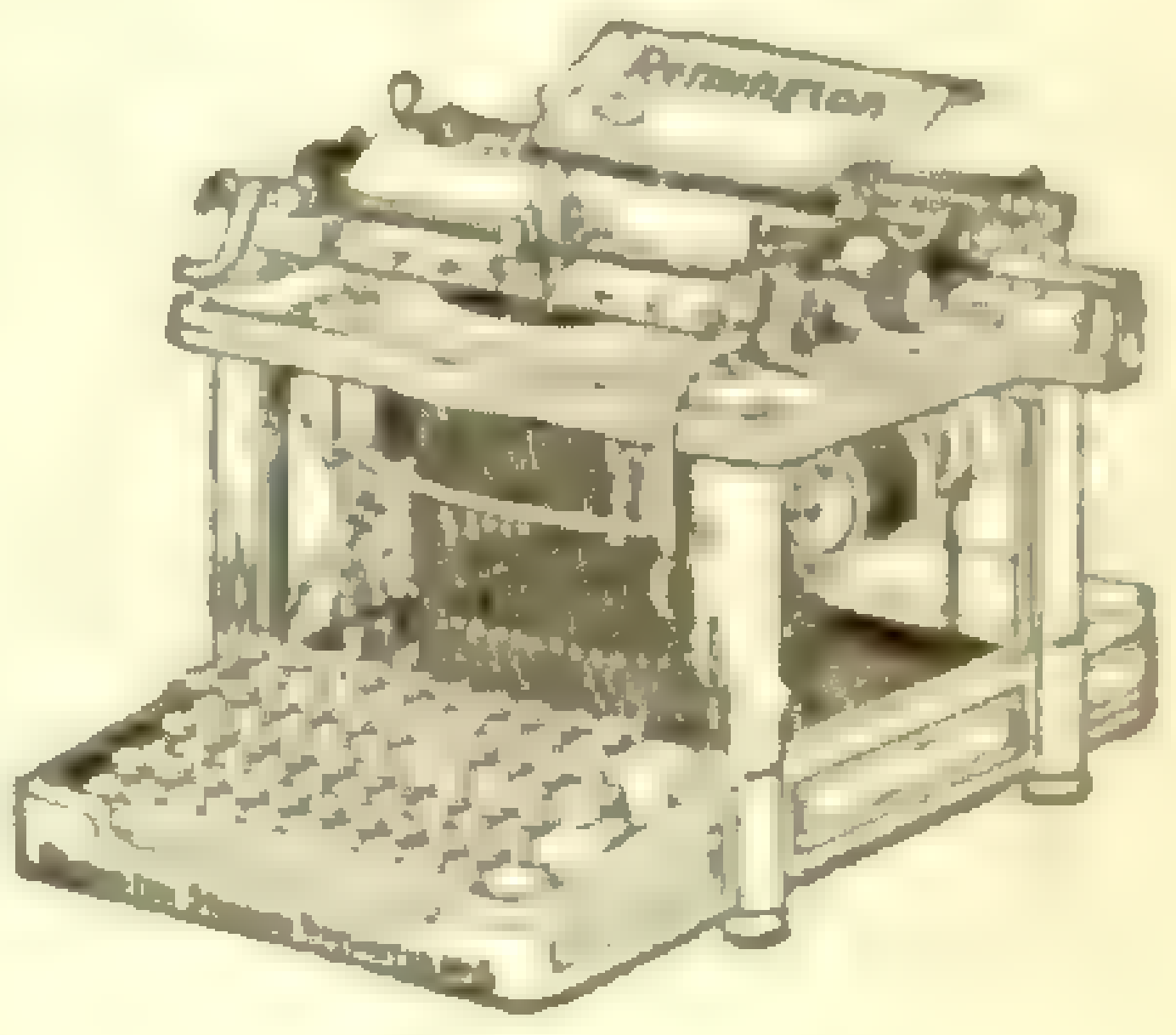

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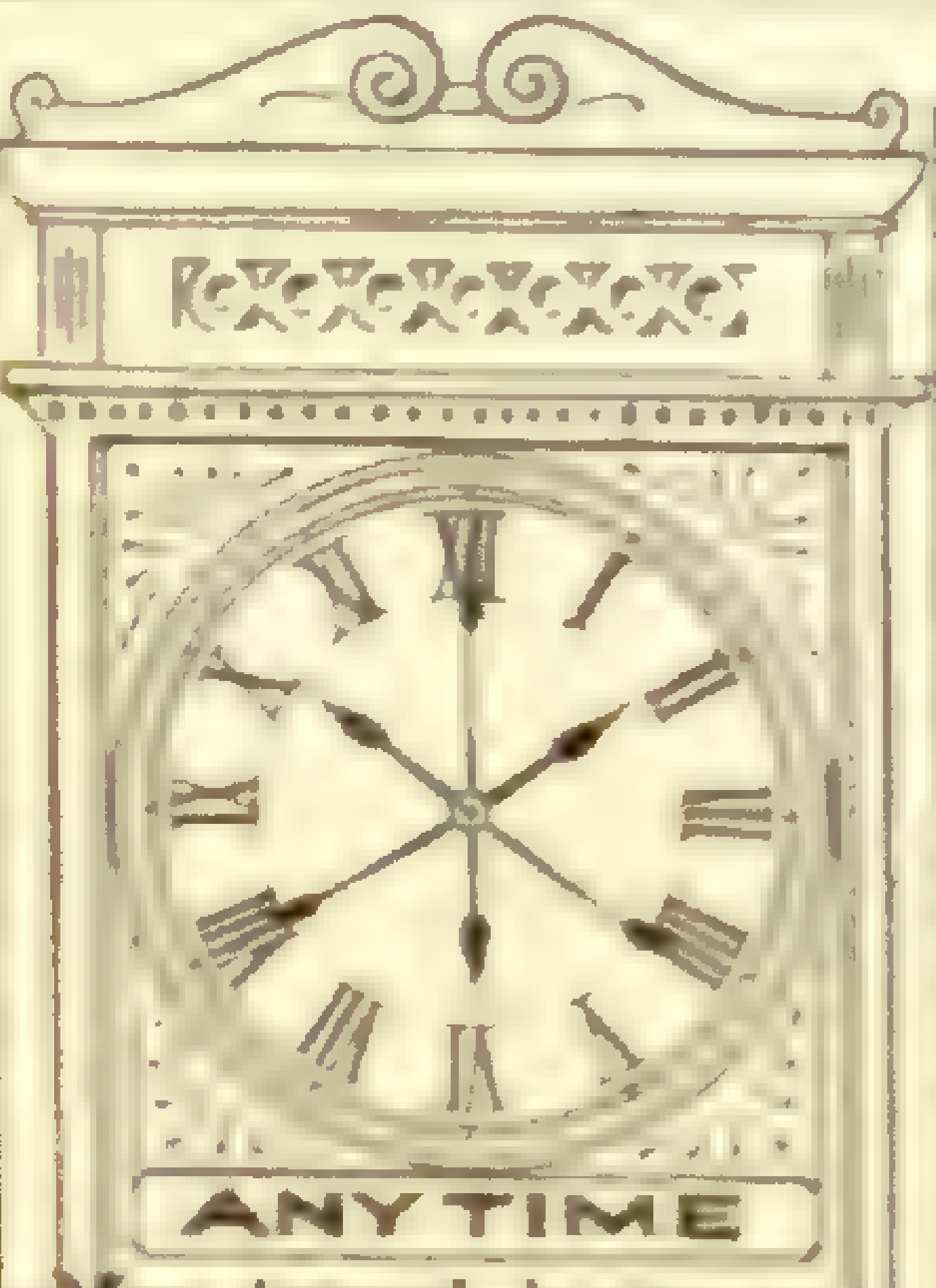

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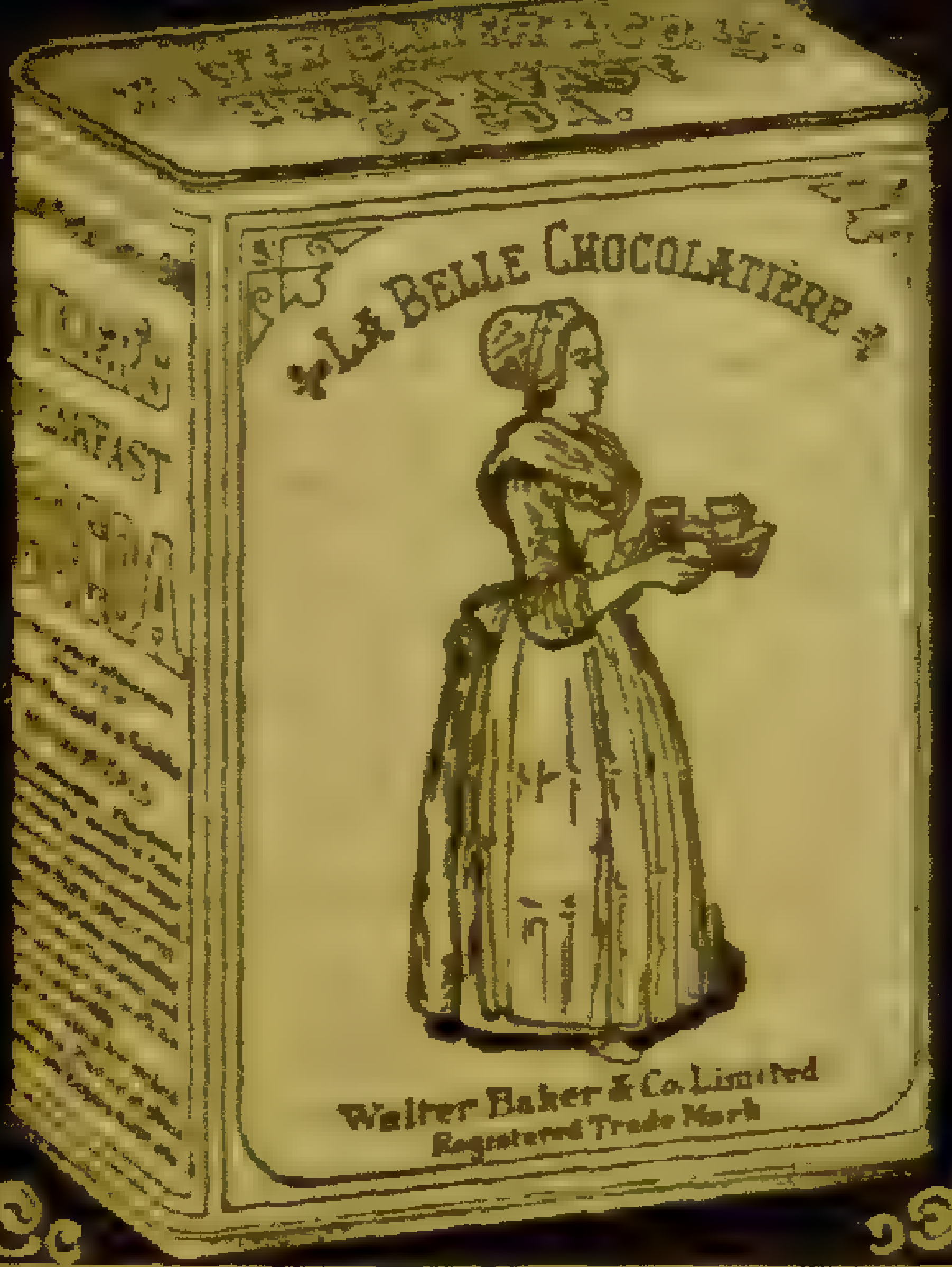

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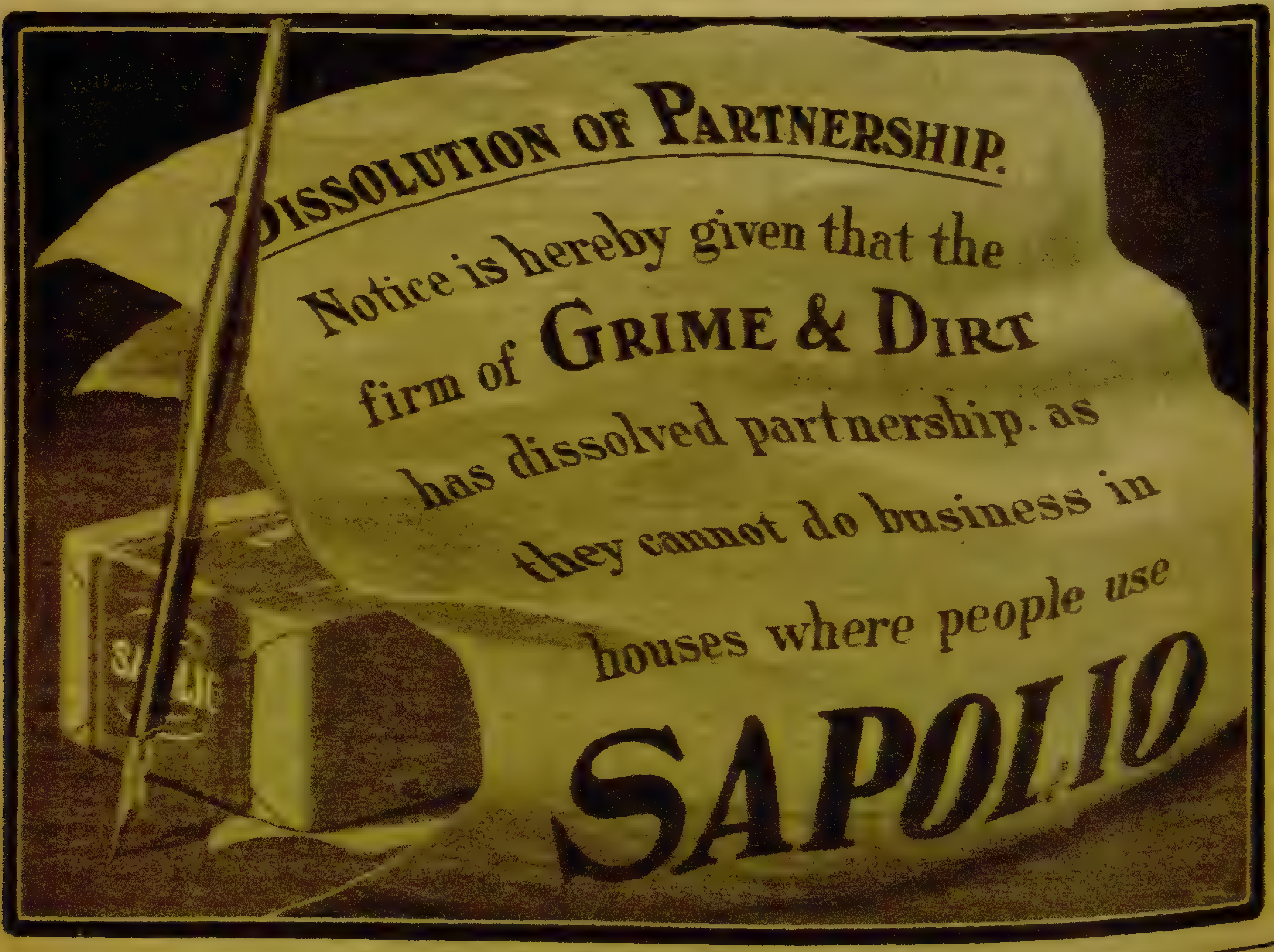

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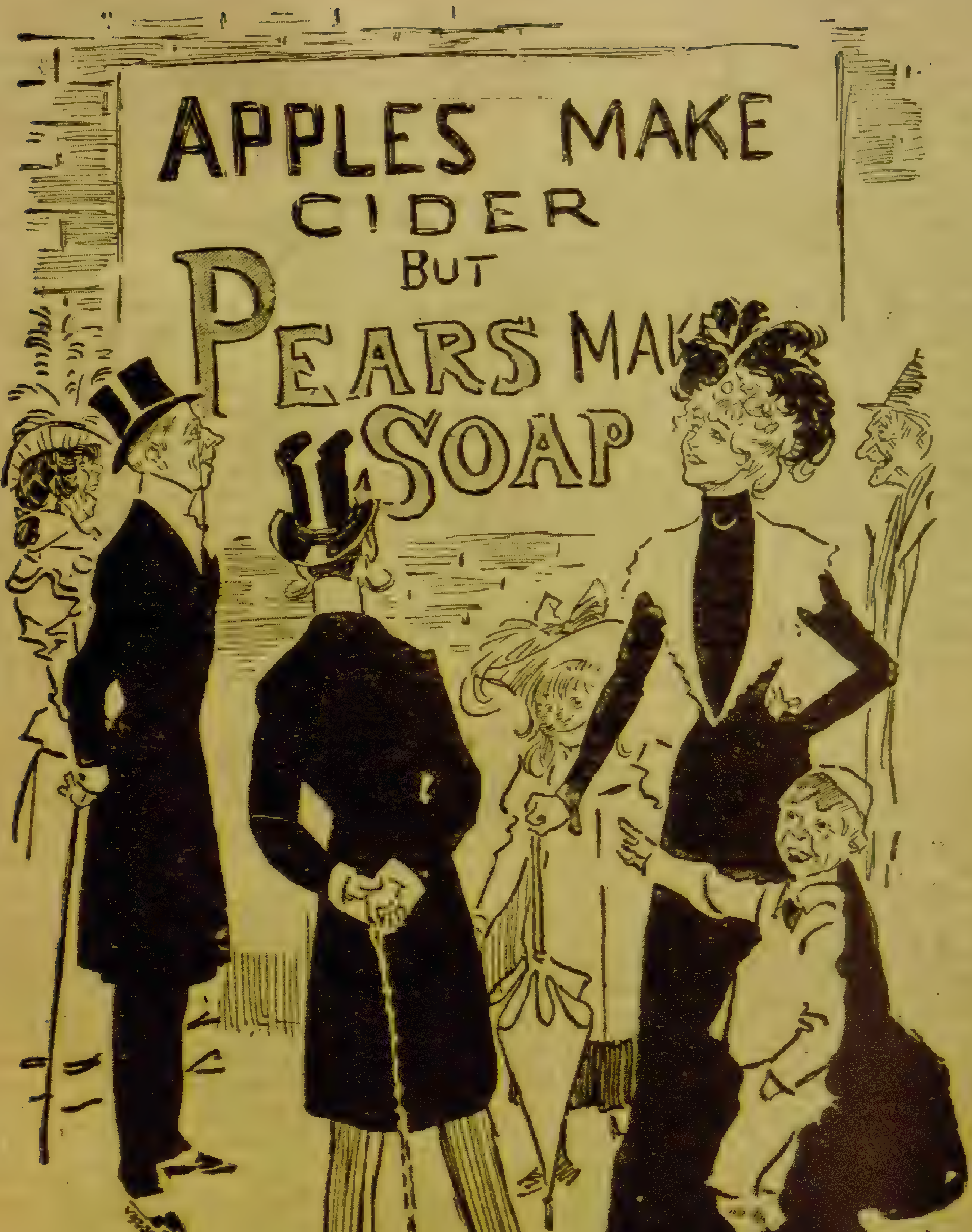
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Vol. XXXII, No. 4 **Issued October 21, 1901**

CONTENTS

THE APPLICATION OF NORMAL SOLUTIONS TO BIOLOGICAL PROBLEMS. *James B. Dandeno* - - - - - - - - - - - 229

GAMETOGENESIS AND FERTILIZATION IN ALBUGO. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX. (WITH PLATES I–IV.) *Frank Lincoln Stevens* 238

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX. (WITH TWENTY-FOUR TEXT FIGURES.) *William L. Bray* - - - - - - - 262

FURTHER NOTES ON THE PHYSIOLOGY OF POLYMORPHISM IN GREEN ALGAE. CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXII. *Burton Edward Livingston* - - - - - - - - - - 292

BRIEFER ARTICLES.

INTRAMOLECULAR RESPIRATION. *T. C. Johnson* - - - - - 303

NOTES ON AQUILEGIA CANADENSIS Linn. and A. VULGARIS Linn. *J. Schneck* - - 304

CURRENT LITERATURE.

BOOK REVIEWS - - - - - - - - - - - - 306

GUIDE TO GARDEN PLANTS

NOTES FOR STUDENTS - - - - - - - - - - 306

NEWS - - - - - - - - - - - - - - 307

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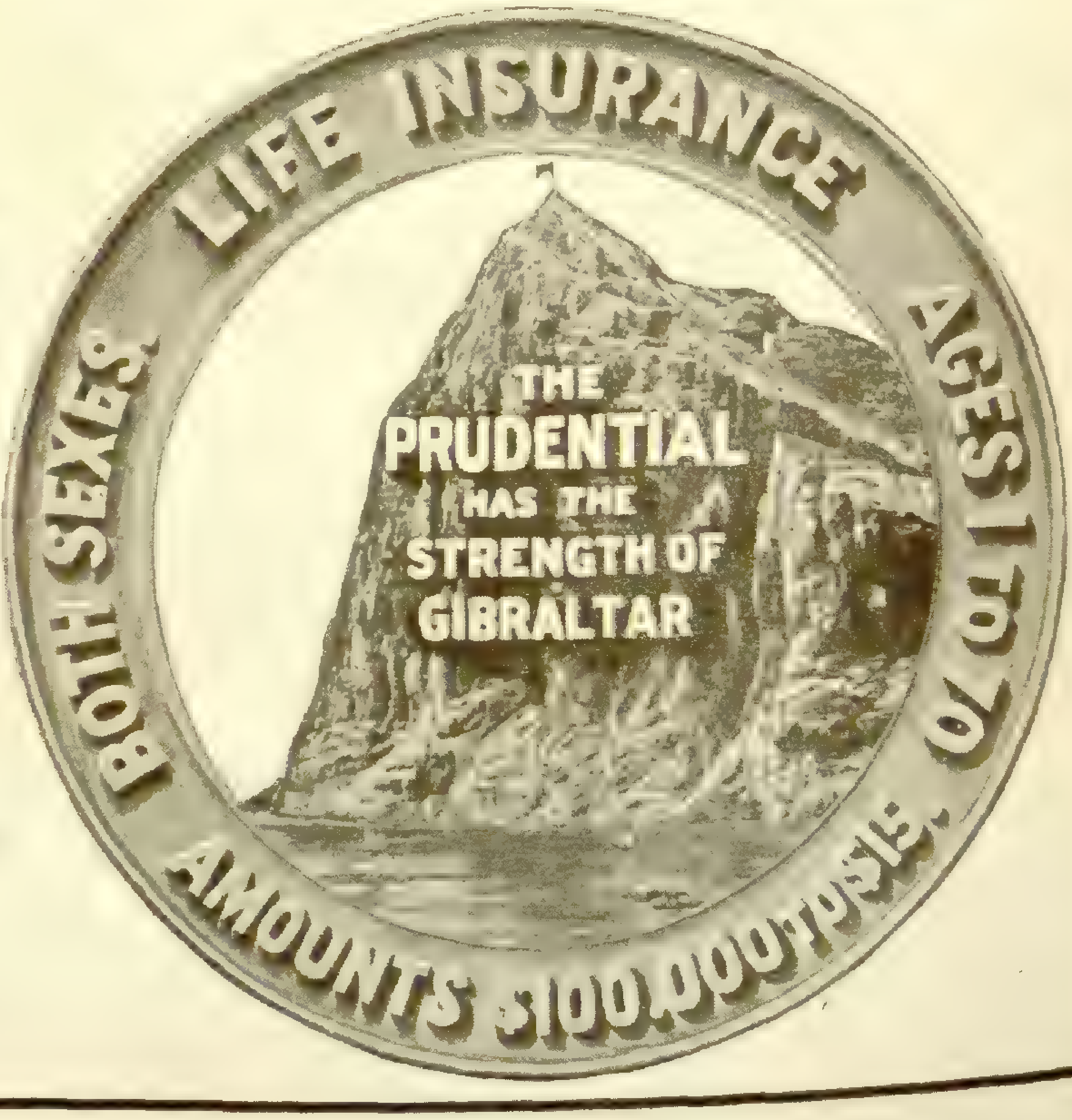
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BOTANICAL GAZETTE

OCTOBER, 1901

THE APPLICATION OF NORMAL SOLUTIONS TO BIOLOGICAL PROBLEMS.

JAMES B. DANDENO.

JUDGING from recent investigations into the effects of ions upon plant and animal life, one is led to conclude that there is much confusion in regard to the interpretation of certain standard chemical solutions. It is not to be doubted that solutions have a very important part in biological functions, and because of their importance it is deemed advisable to attempt to place this branch of an important subject upon a firmer basis.

Since solutions of molecular concentration have been adopted for comparison, in place of the older percentage concentration solutions, there seems to be a great tendency to misinterpretation and confusion. Solutions prepared on the percentage basis are not now considered scientifically accurate when used for purposes of comparison, while those molecularly equivalent may be compared with scientific accuracy. The molecular and the equivalent solutions are the only ones here discussed.

Much of the physiological work done with molecular solutions proves upon examination to be faulty because of a misconception of the meaning of *normal* solutions, *gram-equivalent* per liter solutions, and *gram-molecule* per liter solutions. There are no less than three interpretations of what a normal solution is. One takes it to be a *gram-molecule* per liter of *solution*. Another takes it to be a *gram-equivalent* per liter of *solution*. Still another regards it as a gram-molecule or a gram-equivalent per liter of *water.* Some use the symbol *n* (meaning in chemistry a normal solution) and say nothing about the method of preparation.

There are two probable causes for this confusion. The analytic chemists have differed in their use of solutions. (Allen, *Chem. News* **40**: 239; also *Analyst* **13**: 181, cited by Sutton **18**,[1] p. 28.) Some (a very few) German chemists use a gram-molecule per liter and call it a *normal* solution. By far the greater number of modern analytical chemists, however, use a *gram-equivalent* per liter of *solution* as a normal solution. The physical chemist uses both the above mentioned methods of preparation, but is always clear as to the meaning, and calls only the *gram-equivalent* per liter the *normal* solution. Those who use the chemical symbol *n* without explanation fall under some shadow of doubt arising from the above mentioned confusion. The work, however, may be faultless and the interpretation accurate. The theory of the separation, in aqueous solutions, of the molecules of compounds into ions is now a generally accepted one, and it is partly because of the actions of these ions, and of the dissociation of the molecule into ions, that there is great need of uniformity and of chemical accuracy in the preparation of solutions. Here are some definitions of *normal* solutions.

1. FRESENIUS (**2**, p. 687): "Solutions of such strength that 1000^{cc} contain an amount of acid or base equivalent to one gram of hydrogen are normal solutions, *e. g.*,

HCl,	mol. wt.	36.46,	wt. in	1000^{cc}	of solution	36.46
H_2SO_4,	"	98 ,	"	"	"	49
Na_2CO_3	"	106.08,	"	"	"	53.04"

Fresenius' chemical table (p. 846) is based on the above mentioned method of preparation.

2. SUTTON (**18**, p. 28): "Normal solutions are prepared so that one liter of solution at 16° C. shall contain the hydrogen equivalent of the active reagent in grams ($H = 1$)," *e. g.*:

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[1] See bibliography at end.

HCl	1	mol. wt.	in grams	per liter	of solution
H_2SO_4	$\frac{1}{2}$	"	"	"	"
Na_3PO_4	$\frac{1}{3}$	"	"	"	"
$KMnO_4$	$\frac{1}{5}$	"	"	"	"
$K_2Cr_2O_7$	$\frac{1}{6}$	"	"	"	"(Talbot **19**, p.65)

3. TALBOT (**19**, p. 64): "A normal solution as defined by Mohr (Talbot **19**, pp. 64, 65) contains in one liter 'one equivalent of the active reagent in grams.' The equivalent in grams may be defined as 'that quantity of the active reagent which contains, replaces, unites with, or in any way, directly or indirectly, brings into reaction one gram of hydrogen.'"

MILLER and KILIKANI (**11**, p. 22), state regarding normality of solutions that "like volumes are equivalent to one another."

On the other side of the question, however, there are a few who use gram molecule per liter solutions and call them *normal* solutions. Of these, two perhaps are worth mentioning, Muter and Menschutkins, both cited by Sutton (**18**, p. 28).

In Ostwald's own work (**13**) he uses both gram-equivalent per liter and gram-molecule per liter of solution, but never confuses them. He uses the gram-molecule solutions for demonstrating molecular conductivity, and some of these tables are to be found in his Lehrbuch (**2**, pp. 722–772). Ostwald (**15**, p. 281) gives Kohlrausch's (**6**) table of equivalent quantities (not molecular quantities) for several solutions and enunciates the principle that the *equivalent* conductivity is a direct measure of the velocity of the migration of the ions. Ostwald (**14**, p. 284) uses normal solutions (with table) in regard to surface-tension of solutions, and on pp. 170–172 he uses *molecular* solutions with table of reference for molecular lowering of the vapor-pressure. There are only two instances of different tables used by Ostwald in his work. It will thus be seen that he makes use of both kinds of solutions according as they best suit his particular purpose.

Van't Hoff (**23**, p. 117), referring to Ostwald, uses the term "so-called molecular conductivity," and he uses freely the term normality as applied to solutions. Hittorf's table (Le Blanc **7**,

p. 78), is based on the *gram-equivalent* per liter solution, and Le Blanc (**7**, p. 79), uses the symbol λ to designate *equivalent* conductivity as distinguished from *molecular* conductivity, which is expressed by Ostwald as μ. Moreover, Valson's (**24**) law of the moduli (tables) is based upon gram-equivalent (not molecular) solutions, as well as almost all the analytical *chemical* tables now available.

It is seen that the physical chemist recognizes two kinds of standard solutions, *molecular* solutions and *equivalent* solutions, calling the latter *normal* solutions. The analytical chemist uses one kind of solution, the normal solution, *i. e.*, the gram-equivalent per liter solution.

The mistakes resulting from misinterpretation of *normal* solutions, and from a confusion of the terms *gram-equivalent* and *gram-molecule* per liter will be better understood if a few particular cases be cited. Kahlenberg and True (**5**, p. 85), speak thus: "Chemically equivalent quantities (*i. e.*, molecular quantities) of the different substances were not compared;" also (p. 91), "expressed in gram-molecules or gram-equivalents per liter;" showing that they regard a gram-molecule per liter as exactly the same as a gram-equivalent per liter, which, in the case of many of the substances referred to (*e. g.*, H_2SO_4), is not correct. What brings out more prominently the importance of the error is the fact that the solution of H_2SO_4 (p. 92) was a *normal* solution (purchased from the chemist), that is a gram-equivalent solution, and was thought to be a gram-molecule solution. Their results show that $\frac{1}{6400}$ gram-equivalent per liter of H_2SO_4 is as toxic as $\frac{1}{3200}$ gram-equivalent per liter of HCl. In other words, the experiments seem to prove that the solution of H_2SO_4 was what they *thought it to be*, though what *it was not*. Heald (**4**, p. 125), referring to Kahlenberg and True, states that "in these experiments the solutions were prepared according to gram-equivalents." On pages 119–123 of Kahlenberg and True we find written *gram-mol.* per liter.

Similar mistakes were made by True (**20**, p. 184), where he says, referring to H_2SO_4, "and since it splits off two hydrogen ions from every molecule, it would have, in chemically equivalent quantities, twice the number of H ions found in HCl, and would have its death-limit at one half the concentration of the monobasic acid." This shows clearly that this author regarded chemical equivalent and molecular solutions as the same.

Kahlenberg and True (**5**, p. 6), say: "In the second column is the concentration just allowing growth, expressed in fractions of a gram-equivalent per liter of water." In the column referred to, the limit for H_2SO_4 is $\frac{1}{6400}$, and for $KHSO_4$ is $\frac{1}{6400}$ in equivalent solutions. Since the toxicity of potassium and of SO_4 at this concentration may be neglected (p. 6), the hydrogen in the $KHSO_4$ is as toxic as *twice* as much hydrogen in the case of H_2SO_4, since there is in chemically equivalent quantities of H_2SO_4 and $KHSO_4$ *twice* as much hydrogen in H_2SO_4 as there is in the $KHSO_4$.

Another instance of the error arising from confusing the gram-equivalent per liter with the gram-molecule per liter is shown in the work of Kahlenberg and True (**5**, p. 109). They say, referring to Ostwald (**16**), "the most dilute solutions with which he worked contained one gram-equivalent in 1024 liters." Ostwald's tables in this reference are *not* made on the gram-equivalent per liter plan, but on the *gram-molecule* per liter plan, and he so states (p. 174). "Die folgende Spalte enthalt unter '*m*' den Wert der relativen molekularen Leitfähigkeit; der Wert von μ_∞, auf welchen derselbe bezogen ist, findet sich in der Ueberschrift der Tabelle angegeben." Also p. 171, "Wo μ_s die molekulare Leitfähigkeit bei der Verdünnung v (in Litern auf in Grammolekulargewicht), μ_∞ den Grenzwert derselben bei unendlicher Verdünnung und c eine Konstante bedeutet. Drückt man die molekulare Leitfähigkeit in Bruchtheilen ihres Grenzwertes aus, setzt also $m = \frac{\mu_v}{\mu_\infty}$."

Kahlenberg and True (**5**, p. 115) give in their tables 56, 57, 58, 59, "concentration gm.-equival. per liter," and refer to Ostwald (**16**, p. 380). Now Ostwald's tables (pp. 369–422) are made *not* on the plan gram-equivalent per liter but *gram-molecule* per liter. No comment is necessary. Again Kahlenberg and True (**5**, p. 116), state, "as maleic acid at the dilution 1024 is dissociated 98.2 per cent. and fumaric acid 78.5 per cent., we should expect the latter to be less poisonous than the former if the toxic action be due to the H ions alone." In the table to which they refer we find maleic acid *92.8 per cent.* at 1024 and fumaric acid 78.5 at *2048*. They state further, referring to the two acids mentioned, "we do not place much reliance on the results obtained from these two acids as it is questionable whether the substances were perfectly pure." The discrepancy above referred to suggests another reason for unreliability of results.

True and Hunkel (**22**, p. 326), while using gram-molecule per liter in their paper, made reference to Kahlenberg and True (**5**, p. 92), where the tables are written gram-equivalent per liter. The one kind of table, of course, cannot apply directly to the other.

In regard to the method of preparation of solutions by dissolving a gram-equivalent of the salt, or a gram-molecule of the salt, as the case may be, in a liter of *water*, there is something to be said. Those who have made errors in this way are Pfeffer (**17**, p. 146), Detmer and Moor (**1**, p. 326), Kahlenberg and True (**5**, pp. 85, 87), True (**20**, pp. 184, 185), True (**21**, pp. 410, 411), Heald (**4**, p. 133), Garry (**3**, p. 298), True and Hunkel (**22**, p. 326), and Ostwald (**14**, p. 190). Pfeffer, Detmer and Moor, and Garry called them *normal* solutions. Kahlenberg and True called them gram-molecule solutions and gram-equivalent solutions, apparently interchangeably, but meaning generally molecular solutions. Ostwald is using Tammann's table which states that the solutions are made by dissolving *n* molecular weights, in grams, of the salts in 1000 grams of water.[2]

The objection to the above solutions is not so much to the method of preparing them as to the application to them of chemical or physical tables prepared on a different basis; and to the error arising from their being called by names which mean something different. A solution prepared by dissolving one gram-equivalent in a liter of *water* is quite different in concentration (in the case of strong solutions especially) from that prepared by dissolving one gram-equivalent in a liter of *solution*. The difference is so apparent that explanation is unnecessary.

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[2] MACDOUGAL (**10**, p. 51) says: "A normal solution of ethyl alcohol is made by adding 46 grams of absolute alcohol to a liter of distilled water." This, to be in any sense accurate, should read (after the word alcohol) *to sufficient water to make a liter of solution.* MacDougal's statement produces an error of about 58^{cc} in 1000^{cc}.

The use of the chemical symbol *n* to represent solutions without some explanation as to the method of preparation of the solution, is likely to cause some doubt to be cast upon the work. One will naturally infer that those who use the symbol without explanation are as likely to err as those who use it with explanation, but in making explanation show an error of interpretation; though this inference might be unfair.

Garry (**3**, p. 298) states: "To designate chemically equivalent solutions, the chemist uses fractional parts of the so-called *normal* solutions, *i. e.*, the solution made by dissolving the equivalent gram-molecule in one liter of water." He uses the symbol N to designate his solutions, but if he prepared them after the method indicted above he is not warranted in using the symbol for normal solutions. Chemical tables showing degree of dissociation will, of course, not apply to solutions so made.

True (**20**, p. 186) uses the term *n*-1024 in reference to Ostwald's tables (**16**), but he is not warranted in using this term because Ostwald's tables just referred to are *not* based on *normal* solutions but are molecular solutions. Heald (**4**, p. 138) uses the term *N* and refers to the same page of *Zeitschrift* for degree of dissociation. These tables do not apply.

In the works of Loeb (**9**), D. J. Lingle (**8**), and A. Moore (**12**) the symbol *n* is used to designate the solutions, but no explanation is given, though in the context there are indications that the symbol *n* is properly applied.

The results of the errors and misconceptions just referred to may be much or little according as the points brought out are of little or of much consequence. At all events, there seems need of establishing this part of physiology upon a more secure and accurate basis. The analytical chemists and the physical chemists have done an enormous amount of investigation upon solutions, and they have established tables for various purposes. Their tables and results are convenient, clear, and ready for use; and the only way to make proper use of them is to make the solutions according to the chemist's standard.

Sutton (**18**, p. 28, footnote) gives a piece of excellent advice in the following statement: "Anyhow it is to be hoped that those who communicate processes to the chemical journals, or abstracts of foreign articles for publication, will take care to distinguish between the conflicting systems." If this advice is useful to the chemist, how much more useful should it be to those who are not chemists, but who in their work make use of tables of standard solutions made by the chemists.

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GAMETOGENESIS AND FERTILIZATION IN ALBUGO.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX.

FRANK LINCOLN STEVENS.

(WITH PLATES I–IV)

[*Concluded from p. 169.*]

III. GENERAL CONSIDERATIONS.

OBSERVATIONAL evidence that kinoplasm and trophoplasm (Strasburger 1892) are true morphological elements of the cell has steadily increased, and striking experimental evidence has recently been adduced to confirm this conception (Hottes, *ined.*). In 1892 Strasburger proposed a theory of fertilization founded upon the assumption that sexual cells are incapable of development, owing to a kinoplasmic starvation. This theory was based partly upon observations on Ulothrix, and the relation of the cilia in sexual and asexual cells. Much confirmatory evidence has since been received, and in Strasburger's latest book (1900) the theory is developed more completely. As applied to sexually differentiated cells, the theory postulates kinoplasmic hunger in the female and trophoplasmic hunger in the male. The phenomena attending zonation in Albugo and Peronospora are capable of explanation in the light of Strasburger's theory, and in turn materially strengthen the theory itself. In Albugo and Peronospora the marshaling of the nuclei into a hollow sphere, a most conspicuous phenomenon, is quite inexplicable on the ground of atavism or phylogeny, nor can it have to do with wall-building. Why then do the nuclei habitually leave the ooplasm, apparently to perform no useful function in the periplasm, only to return and function as female pronuclei?

A study of the accompanying plates shows plainly that the periplasm is of a distinctly different character from the ooplasm.

The latter is typically very dense and alveolar, does not stain with gentian-violet but takes the orange G. The former stains darkly with the gentian-violet, and is filar, not alveolar. The processes leading to zonation may indeed be characterized provisionally as a differentiating of the oogonium into two regions, a periplasm rich in kinoplasm, and an oosphere rich in trophoplasm. This statement is borne out by all the positive characters of the trophoplasm and by the stain reaction and structure of the kinoplasm.

The nuclei are in mitosis and do not lose their membrane until zonation is sharp, nor do they reenter the ooplasm until their membrane is lost. The kinoplasmic nuclear membrane is apparently left in the periplasm, and its absence is evident during the second mitosis, thus resulting in that marked difference in character between the first and the second mitosis, which is illustrated in the figures, a difference which was noted in *A. Bliti* in my earlier paper (1899, p. 231). The nuclear membrane in the second mitosis is very thin or perhaps absent; the achromatic figure is weak and consequently often distorted and irregular. Every indication is that of an absence of kinoplasm.

Thus the behavior of both oogonial nuclei and cytoplasm confirms in a striking way the view that kinoplasm is important in sexual differentiation, and suggests that the nuclei pass to the periphery to rid themselves of superfluous kinoplasm, possibly to prevent parthenogenetic development in the oosphere. If this be the true reason for the migration of the nuclei, it logically follows that kinoplasm is not readily convertible into trophoplasm, at least not in the conditions that prevail in these oospheres.

In the antheridium a behavior complementary to that exhibited in the oogonium is seen. The antheridial protoplasm stains intensely with the gentian-violet before fertilization, but after fertilization the cytoplasm left in the antheridium fails to give this reaction. The antheridial nuclei as they lie in the tube possess a heavy membrane and stain darkly, giving every indication that they are rich in kinoplasm. In *A. candida* zonation is not so marked, and the nuclei do not pass to the periplasm during division. In this species, however, there is a great preponderance of trophoplasm, owing to the highly developed coenocentrum, as well as to the fact that the trophoplasm of the whole oosphere is surrendered to one nucleus.

In general, the phenomena of oogenesis and spermatogenesis in Albugo afford remarkable confirmatory evidence for Strasburger's theory of fertilization. If the definite establishment of this theory should occur, botanists will come into more accord with those zoologists who accept the theory of Boveri that the sperm contributes the centrosome (kinoplasm), which is the one element needed by the egg to restore its capacity for division. Possibly the results of Klebs (1896), Loeb (1899), Nathansohn (1900), and others who have artificially induced parthenogenesis, may be explicable in the light of this theory, since it is at least conceivable that the environmental conditions which are supplied in these experiments may be identical with those which favor or retard the development of kinoplasm in the cell. Indeed, the results already attained by Hottes (1900) point in this direction.

No definite separating membrane can be detected in any of the species at the time of zonation, although the delimitation of periplasm and ooplasm is very sharp. Analysis of the condition shows that the differentiation is solely dependent upon the difference in character between the ooplasm and periplasm that has been described in previous paragraphs. It is outside of the ooplasm that the nuclei accumulate, and here in *A. Bliti*, *A. Portulacae*, and *A. Tragopogonis* they divide, some of the daughter nuclei returning to the oosphere.

The plasmoderma is formed at about the time that the primary oospheric nuclei renter, and at a period slightly later evidence of plasmolysis may be found. It appeared possible from some conditions seen in *A. Bliti* (Stevens 1899, *figs. 65–67*) that the nuclei might take some part in the formation of the new plasmoderma, but critical study shows that no constant relation is maintained between mitosis and plasmoderma formation. The plasmoderma appears to arise directly from the cytoplasm in a manner closely resembling that which Mottier (1900) describes as a rearrangement of alveolar planes. The alveolae are here so small that it is impossible to assert with certainty that the processes are identical.

Simultaneous division of the nuclei in oogenesis and spermatogenesis is a phenomenon of wide distribution among the algae and fungi. The simultaneity itself is not remarkable, since it is frequently characteristic of multinucleate masses of cytoplasm, as endosperm nuclei of angiosperms, latex vessels (Pirotta and Buscalioni 1898), and plasmodia. The simultaneity in oogenesis is, however, of quite a different nature. Numerous vegetative nuclei, probably of very different ages, accumulate in the rudimentary sex organs and are there cut off from the parent cell. These nuclei pass simultaneously into mitosis, while the nuclei in the vegetative mycelium do not do so.[5]

This simultaneous mitosis, while it may be regarded with Hartog[6] (1891, p. 23) as a "phylogenetic reminiscence," is still often something more, and in the case of Albugo it is apparently a step necessary to the sexual differentiation of the gametes.

Whether a reduction in chromosomes occurs in connection with this gamete production is uncertain. To be sure Berlese (1898) claims to count the chromosomes during mitosis and fusion, and to establish definitely that reduction occurs in germination. The nuclear phenomena which he describes are so different from the conditions seen by Wager (1896), Davis (1900), and myself (1899), that the evidence must be accepted with reserve. The distinct difference in character between first and second mitosis in Albugo is, as I have said in another part of this paper, probably due to change in kinoplasmic content.

[5] Frequently nuclei in the immediate vicinity of the oogonium show a slight tendency to divide, and may even attain to the spirem stage (Stevens 1899, *fig. 45*).

[6] We can only regard the nuclear divisions in oogonium and antheridium as phylogenetic reminiscences of the formation of gametes by cell division; the periplasm is thus equivalent to a number of degenerate gametes which have taken on the function of epispore formation; the multitude of gametes are sacrificed to the few.

In three species of Albugo there are two mitoses, in another species probably two, in the gametangia; while in Peronospora (Wager 1900) there is only one. In Sphaeroplea (Klebahn 1899) the antheridial nuclei divide repeatedly, while the egg nucleus does not suffer visible change. In Vaucheria, even if there is a division in the oogonium, as seems possible (Oltmanns 1895, p. 392), it is probably not a differentiating division, since all of the nuclei but one wander back to the parent filament, and are presumably capable of vegetative function. From these examples it appears that the number of divisions in both oogenesis and spermatogenesis varies in different species, and differs in the two sexes of the same species; while in some forms there seems to be no mitosis directly concerned in the genesis of the female pronucleus. These conditions render improbable the existence of a reduction in the number of chromosomes during gametogenesis in these algae and fungi. Oogenesis and spermatogenesis begin almost simultaneously for a given pair or group of sex organs, yet all efforts to correlate their inception with any development external to the organs themselves were vain. A comparative study of four species shows no constant relation between the male and female organs in the sequence of their development, which seems to proceed independently in each organ. It is not probable, as might at first seem, that the inception of the antheridial tube is caused by the presence of the oosphere, since *fig. 50* presents a case where the antheridial tube grew and functioned normally, yet without a parallel development in the oogonium, or indeed the existence of an oosphere.

The factor which determines how many primary oospheric nuclei shall enter the ooplasm is uncertain. Clearly the position of the nucleus during its first mitosis determines whether or not one of the daughter nuclei shall enter the ooplasm. Yet this position seems to be governed by no law, the greatest irregularity existing, as is general in cases of simultaneous division in multinucleate masses of cytoplasm. This irregularity is equally prevalent at the time of zonation (*figs. 2, 28*). It is quite possible, therefore, that mere accident determines how many of the nuclei are to be so oriented as to contribute daughter nuclei to the oosphere. It is needless to attribute to the cytoplasm any special selective power which causes definite nuclei or a definite number of them to return, although such selection is exhibited in some plants. For example, in the oogonium of Vaucheria (Oltmanns 1895) one nucleus maintains its position near the beak, amid violent activities of the surrounding cytoplasm, while the chloroplasts and numerous other nuclei are withdrawn. In the oogonium of Peronospora, according to Wager (1900), one nucleus of the many is selected to reenter the ooplasm and function as the female pronucleus.

The elimination of supernumerary nuclei by digestion in the surrounding cytoplasm finds analogy in vegetative cells in the sieve tubes of Pinus (Strumpf 1898); and still more striking in the sexual cells of Achlya (Trow 1899, p. 156), where there is an average of ten times as many nuclei as there are eggs to be produced. The phenomenon is also analogous to that described by Rückert (1892) and Oppel (1892), where several male nuclei enter the egg, the superfluous ones degenerating and functioning as yolk nuclei. In Actinosphaeria Hertwig (1898) also describes a reduction from multinucleate to uninucleate condition before fertilization, which is essentially similar to that seen in Albugo, the supernumerary nuclei being dissolved in the surrounding cytoplasm. In this species, as in Albugo, the nuclei are all alike, showing no such differentiation as is common among the infusoria. The phenomena seen in the Fucaceae (Oltmanns 1889), particularly in *Himanthalia lorea*, may be classed in this same category. Here the cytoplasm in early stages contains eight nuclei, the number being later reduced to one by casting off the seven superfluous ones.

In Vaucheria (Oltmanns 1895) the reduction from a multinucleate to a uninucleate condition is effected in quite a different manner, by protoplasmic streaming, the supernumerary nuclei being carried back into the parent hypha. Thus the reduction occurs before the oosphere is differentiated, and not in the ooplasm proper. Klebahn (1899) describes in Sphaeroplea a case where the reduction from the multinucleate to the uninucleate condition does not occur until after fertilization, even if then, there being several nuclei in the oosphere only one of which is fertilized. The nuclei which receive no sperms are recognized in later stages by their smaller chromatin content, but their fate on germination was not followed. Golenkin (1900) agrees with Klebahn in finding a multinucleate egg, one nucleus of which functions; but Golenkin says that the nuclei then all fuse into one. Such a condition offers serious difficulties of interpretation in the light of the present theories regarding the cell. Since uninucleate oospheres were present among the multinucleate ones, it is possible that the condition observed by Golenkin was pathologic, a view which is strengthened by the fact that he was unable to germinate the spores after two years' trial.

In Saprolegniaceae Trow (1895, p. 630, and 1898, p. 166) notes a clumping or possibly pairing of the nuclei as they degenerate. I have also noted this phenomenon in the foregoing pages. Yet this is in no way to be confounded with the process of general fusion as described by Hartog (1891, p. 25) and Golenkin (1900), since these writers derive a functional nucleus from the ultimate result of successive fusions, while in the case observed by Trow, and in that seen by the writer, the nuclei thus appearing to fuse are really in the process of degeneration.

Inasmuch as it has been possible in all cases to follow the parallel development of the oospheres, it can hardly be doubted that in *A. Tragopogonis* and *A. candida*, as in Achlya, the Fucaceae, etc., the supernumerary nuclei represent potential pronuclei, and that each nucleus in the oosphere or *A. Tragopogonis* and *A. candida* is homologous with one of the nuclei in the oosphere of *A. Bliti* or *A. Portulacae.*

The coenocentrum has to some extent been discussed in connection with the description of *A. Tragopogonis* and *A. candida.* It yet remains to compare the structure in the different species. In *A. Portulacae* it is least developed, consisting simply of a large zone of darkly staining cytoplasm which contains at its center the alveolar (trophoplasmic) region. This region seldom contains a globule such as characterizes the other three species. In *A. Bliti* the structure is much more prominent and endures for a longer period. It is of more complicated structure than in *A. Portulacae*, owing to the presence of a distinct central globule. In *A. Tragopogonis* the coenocentrum is still more highly developed. The central globule seems to be formed by the trophoplasm of the central region, or rather by the coalescence of the contents of its vacuoles. This globule in a later period becomes granular, the granules staining like nucleoli. *A. candida* possesses the most highly developed coenocentrum which, while closely resembling that of *A. Tragopogonis*, differs in that from its earliest formation till near the end of its functional activity it is thickly beset with coarse granules (*figs. 13, 17*) that in size and stain reaction agree with the nucleoli of this species.

In its function as well as structure this organ advances in complexity in the series here presented. In *A. Portulacae* there is no extensive accumulation of nutrient material in the vacuoles of the trophoplasm. In *A. Bliti* this accumulation is marked. In *A. Tragopogonis* the central globule shows strong chemotactic attraction for the nuclei and serves as nourishment for one or more of them. In *A. candida* this function of nutrition reaches greater perfection, as is shown by the attachment of the nuclei to the coenocentrum rather than their mere approximation to it. The coenocentrum develops earlier in the more highly differentiated species, and thus by exerting its attractive influence upon the nuclei before zonation strongly influences ontogeny. It has likewise probably been an important factor in changing the general character of oogenesis in phylogeny.

The presence of the receptive papilla in the four species of Albugo, as well as in Peronospora (Wager 1900, p. 270), attests to its importance either in the present or in ancestral species. Young stages in the development of this structure show that the plasmoderma adheres to the wall immediately under the developing papilla, and exhibits a granular cytoplasm at this point. The granulation probably indicates the presence of a cellulose enzyme, formed here to soften the wall which alters chemically, as is evidenced by its response to stains and by its swollen condition (Stevens 1899, *figs. 47, 50*). The antheridial tube at this stage of development is probably unable to penetrate the cellulose wall of the oogonium, and that duty rests with the female cell.

Perhaps this curious structure can better be interpreted by a glance at possible ancestral forms. In algal aquatic forms, in which the gametangia open into the water, each sex organ opens independently, the female usually first. If the Peronosporeae have been derived from some such ancestors and these habits have been retained, in species where the walls of the antheridium and oogonium are in contact the origin of the receptive papilla is clear. Gametangia are usually of greatest turgor at the time of opening; therefore, in the present case the bulging, consequent upon the softening of the partition wall, is from the oogonium toward the antheridium. The formation of the receptive papilla in Albugo occurs immediately before the maturity of the oosphere, precisely as does the analogous phenomenon in Vaucheria.

The term "receptive papilla" is a misnomer, since this is not in any morphological sense a receptive structure, nor is it homologous with the receptive spot of the egg. In one case the differentiated area is part of an egg and functions as a place of reception for the sperm (as the eggs of Sphaeroplea, Saprolegnia, Oedogonium, etc.); in another case it is a zymogenic region of the protoplast adjacent to the point where an opening is to be made in an oogonial wall, either to furnish exit for the female gametes or for the entrance of the male elements, and is homologous with the opening spot of sporangia generally, as Cladophora, Bryopsis, Sphaeroplea, and Oedogonium. In the Saprolegniaceae the papilla does not furnish the place of entrance for the antheridium tube, although in Albugo it does (Zopf 1890, p. 293). The two regions occasion no danger of confusion in the case of the multiovulate (vieleiig) oogonia, nor in cases where the egg is clearly differentiated in a surrounding periplasm; neither should they in forms like Vaucheria and Oedogonium.

The migration of antheridial nuclei into the tube seems to be independent of the developmental condition and metabolic activity of the oogonium, and is probably due to a negative rather than positive chemotropism, possibly of such a nature as that suggested by Hartog (1888) for the sporangia of the Saprolegniaceae. The objections raised by Humphrey (1892) to Hartog's view do not find application here, since he was considering cases where the sporangium failed to expel any of its spores. In Pyronema, where a condition similar to that of Albugo often prevails, Harper (1900, p. 362) explains the migration of some antheridial nuclei and the passivity of others by assuming that "the chemotactic or other stimulus which leads the male nuclei to migrate through the tube to the oogonium would in this case be assumed to have exhausted itself when a number equal to the number of egg nuclei had reached the oogonium." Such an hypothesis does not appear adequate for Albugo, for to assume that a stimulus which can arouse a given number of nuclei to migrate cannot bring the same activity to a greater number presents serious difficulties, and the supernumerary males are not found *en route*, as would be the case if they were stopped when the female nuclei have consorts and the hypothetical stimulating agent has been exhausted. The failure of some nuclei to leave the antheridium is more probably due to a lack of irritability on the part of some sperms than to a lack of the stimulating substance.

The phenomenon of the passage of nuclei from the body of the antheridium into its tube is no more comparable to the seeking of the female by a sperm than is the emptying of an algal sporangium, or an antheridium of the mosses or ferns, or the passage of the nuclei and cytoplasm from a pollen grain into the tube, all of which are clearly independent of chemotactic influence originating in organs of opposite sex, inasmuch as they can occur in the entire absence of the female. It is after expulsion from the paternal gametangium that the chemotactic influence of the female unit is exerted upon the males. In the ferns, mosses, and most algae the chemotactic influence of the female extends over a comparatively wide region. In the spermatophytes the area is much restricted, since the pollen tube opens near the oosphere. In the Albuginaceae, where the male gametangium opens directly into the female gametangium, the region over which this influence may be exerted is still more limited. Indeed it may be questioned whether the force which brings the nuclei of the coenogametes (Davis 1900) together in pairs is at all the same as that which brings gametes together in the open. The pairing of nuclei in multinucleate masses of cytoplasm is comparable to the pairing of the male and female nuclei after the sperm has entered the cytoplasm of the egg, as is readily apparent from a consideration of the conditions presented in the larger eggs, as Fucus. Pfeffer demonstrated that the gametes in the open are drawn together by chemotactic attraction, and Wilson (1900) assumes that a similar attraction brings the nuclei together in the cytoplasm of the egg. Apparently two different forces operate, one to bring the sperm to the egg and induce penetration, the other to bring the pronuclei together in the ooplasm. Conklin (1899) has already distinguished these as distinct factors, and attempts to prove that in some cases at least cytoplasmic currents are responsible for the movement of the nuclei in the cytoplasm. Such an explanation does not seem adequate for the multinucleate oosphere of Albugo, as it would involve complexity inconceivably great. An explanation resting on chemotaxis is more tenable.

Conditions where an antheridial tube has reached the oosphere after that organ has been fertilized by another tube (*fig. 48*), as well as cases where two tubes open into one oosphere (*fig. 51*), show there is no correlation between the number of female nuclei to be fertilized and the number of nuclei which pass from the antheridial tube. This is also emphasized in *fig. 50*, where a tube is opening into an oogonium having no oosphere, and into which an abundance of nuclei are poured. From these conditions, as well as direct observation, it is clear that the number of males and females is not exactly equal. In *A. Tragopogonis* unpaired male pronuclei are sometimes seen in the fertilized oosphere, but they are eventually digested by the ooplasm. Similarly, those male nuclei which do not pass into the antheridial tube, and those lying in an antheridium which forms no tube, fail to resume vegetative function and may be found *in situ* in stages of degeneration. The inability of such nuclei to function vegetatively attests their sexual differentiation and accounts for their subsequent rapid elimination.

One observation may help to disclose the force which directs the antheridial tube in its penetration of the oosphere. Two abnormal oospheres were seen quite devoid of nuclei. In one of these only the plasmoderma was developed (*fig. 52*), in the other periplasm and ooplasm were separated by a wall. In both cases the only antheridial tube present had gone astray in the periplasm. The absence of oospheric nuclei and the misdirection of the tube in the same oosphere may be only a peculiar coincidence.

Immediately after the opening of the antheridial tube a wall is seen surrounding the oospore. This develops with great rapidity, often attaining considerable thickness before the pronuclei have begun to fuse. Later thick walls, composed principally of cellulose for the nourishment of the germinating spore, are laid down from the inside, and on the outside heavy brown walls which are characteristically corrugated.[7]

In teratological forms, which abound in all species of Albugo, antheridial tubes where they lie in contact with the periplasm are frequently seen coated with the characteristic pectiniferous deposit. This occurrence was noted by DeBary (1863), and mention of it is frequently found in works on the morphology of the group. Occasionally I have found isolated balls of this pectiniferous deposit lying in the periplasm. These observations in a measure confirm the generally accepted belief that the outer wall is laid down by the periplasm, a view originally proposed by DeBary (1863).

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[7] For brevity I shall hereafter use the term *pectiniferous* to designate this characteristic brown coating, inasmuch as pectin seems to be the constituent which is present here and absent from the other parts of the fungus. From the literature at hand the deposit appears to be really a mixture of cellulose, callose, cutin, and pectin, although its actual composition is yet open to question (Magnin 1895, Zalewski 1883).

Sometimes an antheridial tube penetrates an oogonium that has not yet differentiated periplasm from ooplasm (*fig. 43*). In such case it often becomes coated with the characteristic pectiniferous wall of the species. More frequently it is aborted, reaching a length not greater than one-fifth the diameter of the oogonium. In such cases the adjacent oogonial walls and the remains of the aborted tube receive a pectiniferous coat (*figs. 44-46*). These phenomena tend to prove that undifferentiated cytoplasm of the oogonium has the ability to form the pectiniferous layer, and that in the absence of the plasmoderma of the oosphere it is apparently a matter of indifference what plasmoderma is to receive the deposit, although the pectin is laid down in contact with or by means of some plasmoderma or tonoplast in all cases.

Oogonia containing many small pectiniferous spheres (*fig. 46*) are quite frequently found, but the origin of the spheres cannot with certainty be determined. They are always accompanied by an aborted antheridial tube, and it may well be that these pectiniferous spheres represent deposits upon the lining membrane of vacuoles, thus emphasizing the similarity between the tonoplast and the plasmoderma in accord with the view of DeVries and Pfeffer. The fact that an aborted antheridial tube is present suggests that a stimulus may emanate from the antheridium which arouses the protoplasm to pectin production. This idea receives further support when it is recognized that the formation of the pectiniferous deposit begins and is most prominent near the antheridial tube (*fig. 44*). It thus often results in the tube becoming incrusted in a pectiniferous wall. *Fig. 45* represents an oogonium prematurely penetrated by two antheridial tubes from opposite ends. These tubes have aborted, but each is accompanied by a pectiniferous formation from which the middle region of the oogonium is exempt.

Occasionally, by the formation of the oospore wall, a supernumerary antheridial tube is pushed aside in the periplasm. It then swells until it assumes a club-shaped appearance as it presses against the wall. In such cases the pectiniferous layer is formed over the whole mass, consisting of the mass of sperm nuclei and the remains of the antheridial tube (*fig. 48*). Conditions like these result, in the ripe spore, in a structure which looks much as though an antheridium lying beside an oospore had been encased (*fig. 49*). Such malformations may be distinguished from antheridia by the still persistent oogonial wall, which would of course not include the antheridium, but do include these masses.

If emanations from the antheridial tube stimulate the cytoplasm of the oogonium to form the pectiniferous layer, why does not the tube become coated as it penetrates the oosphere? This question probably receives its answer in the fact that the ooplasm has not the power to form pectin. It produces cellulose deposits, but not even in teratological cases (*fig. 47*) does it give evidence of any ability to form the pectiniferous layer. It is also notable that the ability to deposit the characteristic thick cellulose layer and to accumulate the typical oily globules is limited to the ooplasm. It seems, therefore, that in the activities leading to zonation there is a differentiation of the cytoplasm, that a capability vested in the oogonial cytoplasm is lost to the ooplasm, and its manifestation in later stages becomes limited to the periplasmic regions.[8] Whether this differentiation consists merely in a shifting of partially elaborated products of metabolism or in a segregation of living cytoplasm into two regions, one possessing a different constitution from the other, must be left an open question.

The stimulating effect from the antheridium may be manifested when the tube has penetrated only half way to the center of the oosphere without emptying, the stimulating agent presumably passing through the wall of the tube when this becomes very thin. The conditions justify the hypothesis that the protoplasm of the oogonium, or the periplasm as the case may be, contains the food constituents needed for the rather extensive production of the pectiniferous deposit, and that the substance contributed by the antheridial tube is more properly comparable to an enzyme than a food. It is a stimulant to activity rather than a material to act or to be acted upon. The protoplasm of the antheridium of Albugo, moreover, seems never to produce pectin, thus favoring the hypothesis that the necessary food materials are limited to the protoplasm of the oogonium.

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[8] The figures of Magnin (1895, *fig. 11*) might at first glance appear to contradic this, but Magnin's figures represent callose which is really present both in inner and outer walls.

The antheridial tube in normal conditions opens near the center of the oosphere, from whence the stimulating agent diffuses outward, awakening no response in the ooplasm because this is incapable of response. When this stimulating agent reaches the oospheric plasmoderma it meets the periplasm, which immediately lays down the rudiment of the outer wall. The fact that the tube opens in the center of the oosphere explains the absence of pectin formation in the periplasm, since the large area of the oospheric plasmoderma is ample to receive all the pectin that is to be laid down. Moreover, the thickening wall probably retards the passage of the stimulating agent into the periplasm, so that the peripheral portion of the periplasm is not incited to formation of the pectiniferous layer, and therefore the oogonial wall receives no pectiniferous coat. An answer to the question originally propounded by Cornu (1872) "si ce plasma extérieur a la propriété de se déposer en couche membraneuse, sans être élaboré au préabable, pourquoi ne se dépose-t-il pas aussi sur les parvis d l'oogone?" is thus suggested.

Normally it is the periplasm that responds to the stimulus, and the periplasm is bounded by its own plasmoderma and contains its own nuclei. It is an independent unit distinct from the oosphere, although it is destined to sacrifice itself for the protection of the oospore in a manner analogous to the tapetal cells in many pteridophytes (Strasburger 1889). Normally, therefore, the production of pectin in Albugo is analogous to the so-called secondary effects of fertilization commonly seen in the higher plants, since it is an effect manifested by a cell other than those directly concerned in the act of fertilization.

SUMMARY OF SECTIONS II AND III.

The processes leading to zonation may be regarded as the differentiation of an ooplasm rich in trophoplasm. The nuclei pass outward, possibly to leave part of their kinoplasm outside of the ooplasm, in order to lessen the possibility of parthenogenetic development. The antheridial nuclei give evidence of heightened kinoplasmic content.

The cell plate is formed, without the participation of the nuclei, by a rearrangement of alevolar planes.

The simultaneous mitosis in gametogenesis is a phylogenetic reminiscence, and was of value in ancestral forms in increasing the number of gametes.

No constant time relation is maintained between the phases of oogenesis and spermatogenesis, but each after its inception seems to proceed independent of the other.

The orientation of the nuclear figure determines which, and consequently how many, primary oospheric nuclei shall enter the oosphere. This orientation seems to be merely accidental.

The supernumerary nuclei are phylogenetically gametes, and their dissolution finds analogy in the Saprolegniaceae and Fucaceae, in Actinosphaeria, and in cases of physiological polyspermy.

The receptive papilla is the result of a softening of the oogonial wall by the oogonial contents, accompanied by high turgor in the oogonium. It is probably a vestigial character recalling an algal ancestry. It is a structure of the oogonium, and therefore is not homologous with the receptive spot, which is a differentiated region of the oosphere.

The migration of the sperms from the antheridium is homologous with the emptying of a sporangium, rather than with the seeking of the female by a male. The number of antheridial nuclei which migrate into the oosphere bears no constant relation to the number of waiting female nuclei. The failure of some nuclei to leave is probably due to a lack of irritability.

Superfluous nuclei of either sex which cannot resume vegetative function degenerate.

The periplasm has the ability to form the pectiniferous deposit, but the differentiated ooplasm cannot. Emanations from the antheridial tube seem to be needed to stimulate the ooplasm to this activity. The pectiniferous layer is deposited on or by a plasmoderma or tonoplast.

The four species, *A. Portulacae*, *A. Bliti*, *A. Tragopogonis*, and *A. candida* constitute a series in which the coenocentrum increases in complexity, the receptive papilla decreases, and the number of functional nuclei decreases. Of these *A. Portulacae* is probably the most primitive, and *A. candida* the most highly specialized form.

The coenocentrum was an important factor in evolution from the multinucleate to the uninucleate condition of oosphere.

The division of the fusion nucleus before passing to the winter condition is a consequence of the uninucleate condition, and constitutes the initial step in germination.

Delay in the division of the fusion nucleus in a uninucleate oospore is associated with retarded and slow fusion of the sexual nuclei, and is explicable as a consequence of slowness in completion of the last steps of fusion.

The relation between Albugo, Peronospora, and Saprolegnia is emphasized by their cytological character, and all are probably derived from a common ancestor having a multinucleate oosphere. The derivation of Peronospora and Saprolegnia from the Chytridineae is rendered improbable.

Pythium is more closely related to the Albuginaceae than to the Saprolegniaceae.

The peripheral gathering of the protoplasm in the oogonium of Saprolegnia may indicate closer relation to Peronospora than to Albugo.

If the Phycomycetes are related to Vaucheria it is from a period before the attainment of the uninucleate oosphere by Vaucheria.

The coenogamete is homologous with some or all of the gametes of a plurigametic gametangium, not with the individual gametes of such a structure.

There is a remarkable agreement between Albugo and Pyronema in many details.

The coenogamete is a result of pushing the synplast habit from the vegetative body into the reproductive organs.

The synplast of the Phycomycetes is a unit in both morphological and physiological sense, although it is philogenetically the equivalent of many units.

BOTANICAL INSTITUTE, BONN.

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EXPLANATION OF PLATES I–IV.

All figures are from material killed in chrom-acetic acid and stained with Flemming's triple stain. The figures were sketched with the aid of an Abbé camera, using the Leitz $\frac{1}{16}$ objective, aperture 1.30, and oculars 1 and 4.

PLATE I. Albugo Portulacae.

FIG. 1. Early stage in massing of protoplasm; nuclei in advanced prophase; receptive papilla prominent. × 857.

FIG. 2. Later stage in oogenesis; nuclei near metaphase; ooplasm and periplasm of very different structure, but not sharply delimited. × 857.

FIG. 3. Zonation; nuclei in metaphase; ooplasm and periplasm sharply differentiated; coenocentrum prominent, consisting of a loosely vacuolate center surrounded by a denser, slightly granular region which stains darker with the orange G. × 857.

FIG. 4. Slightly later than *fig. 3*; primary oospheric nuclei entering oosphere; ooplasm and periplasm sharply delimited; ooplasm typically alveolar, staining very lightly with orange G; periplasm staining densely with gentian violet, filar in structure; three reentering nuclei show each a very weak but distinct polar ray; coenocentrum has disappeared. × 857.

FIG. 5. Primary oospheric nuclei before second division; receptive papilla very prominent; later than *fig. 4*. × 857.

FIG. 6. Receptive papilla open; oospheric nuclei in second mitosis. × 857.

FIG. 7. Antheridial tube in oblique section showing many nuclei and no walls; oospheric nuclei in second mitosis. × 857.

FIG. 8. Antheridial tube in section slightly oblique; sperm nuclei numerous, elongated; stage slightly older than in *fig. 7*. × 1366.

FIG. 9. Transverse section of the antheridial tube, showing its multinucleate character. Oosphere of about the age shown in *fig.* 7. × 1366.

FIG. 10. Nuclei pairing after opening of antheridial tube, a distinct wall surrounding oospore; remains of antheridial tube visible in periplasm; degenerating nuclei in antheridium. × 857.

FIG. 11. Fusion complete; stage before accumulation of oils and before the outer walls are complete. × 857.

FIG. 12. Portion of mature wall. × 857.

PLATE II. Albugo Candida.

FIG. 13. Very young coenocentrum showing that the granules pass in from the surrounding ooplasm; oosphere slightly younger than stage next shown. × 1366.

FIG. 14. Early oogenesis; oosphere roughly outlined by a withdrawal of the protoplasm from the oogonium wall, leaving only a loose periplasm behind; nuclei approximately in metaphase; coenocentrum well developed. × 1366.

FIG. 15. After first division; several nuclei clustered around the coenocentrum; some already gone to the periplasm. × 1366.

FIG. 16. Later than *fig. 15;* nearly all of the nuclei have retreated to the periplasm; those remaining in the ooplasm in mitosis. × 1366.

FIG. 17. Later than *fig. 16;* mitosis complete. × 1366.

FIG. 18. Very slightly later than *fig. 13;* nucleus in metaphase, elongated owing to attraction by coenocentrum; coenocentrum densely and coarsely granular. × 1366.

FIG. 19. Two nuclei attached to coenocentrum; one in late anaphase, the other in telophase; coenocentrum more dense than in *fig. 18;* oosphere similar to that shown in *fig. 14.* × 1366.

FIG. 20. Similar to *fig. 19;* one nucleus in late anaphase attached to coenocentrum. × 1366.

FIGS. 21, 22. One nucleus much enlarged attached to coenocentrum by a pseudopodium-like extension; all other nuclei lie in the periplasm. × 1366.

FIG. 23. Before fusion; male and female nuclei and a supernumerary nucleus near the coenocentrum. × 1366.

FIG. 24. Metaphase of first division of fusion nucleus. × 1366.

FIG. 25. Anaphase of first division of fusion nucleus. × 1366.

FIG. 26. An antheridial tube bearing two nuclei; the female nucleus lying in the ooplasm near the coenocentrum. × 1366.

PLATE III. Albugo Tragopogonis.

FIG. 27. Early stage of oogenesis; protoplasm collected in one central mass; nuclei approaching metaphase; a slight indication of the coenocentrum apparent in the center. × 857.

FIG. 28. Condition slightly later than *fig. 27;* oogonium just before zonation; nuclei approximately at metaphase in both oogonium and antheridium; no sharp separation between ooplasm and periplasm. × 857.

FIG. 29. Slightly later than *fig. 28;* anaphase of first division; daughter nuclei entering ooplasm; ooplasm and periplasm sharply differentiated. × 1366.

FIG. 30. Immediately after the first division; primary oospheric nuclei moving toward coenocentrum, two of them strongly elongated; differentiation between ooplasm and periplasm sharp; plasmoderma probably present and many periplasmic nuclei pressing against it; coenocentrum prominent. × 857.

FIG. 31. Slightly later than *fig. 30;* ooplasm and periplasm separated by definite plasmoderma; oosphere multinucleate; coenocentrum contracted to a spherical homogeneous globule surrounded by dense protoplasm; primary oospheric nuclei attracted by coenocentrum. × 857.

FIG. 32. Metaphase of second mitosis; several nuclei attached to the coenocentrum; periplasmic nuclei not dividing; plasmoderma well defined; coenocentrum staining darkly and not homogeneous. × 857.

FIG. 33. Antheridial tube nearly ready to open, bearing several nuclei; oosphere in same condition as shown in *fig. 32, i. e.,* nuclei in second mitosis. × 1366.

FIG. 34. Similar to *fig. 32;* nuclei in second anaphase; ten dividing nuclei discernible in this one section. × 857.

FIG. 35. One female nucleus lying beside the coenocentrum—somewhat larger than daughter nuclei of second division; general appearance of the oosphere much like that in *fig. 36.* × 1366.

FIG. 36. After the opening of the antheridial tube; definite wall surrounding oosphere; remains of antheridial tube in oosphere; female nucleus in resting condition much larger than in *fig. 35* and lying beside the remains of the coenocentrum, which has lost its characteristic form; sperm nucleus somewhat elongated. × 857.

FIG. 37. Male and female nuclei lying in contact, both in resting condition, enveloped by the remains of coenocentrum; male larger than in earlier stages; compare *figs. 35, 36.* × 1366.

FIG. 38. Similar to *fig. 37;* also showing degenerate nuclei from same oosphere. × 1366.

FIG. 39. Fusion nucleus and remains of coenocentrum. × 1366.

FIG. 40. Anaphase of first division of fusion nucleus. × 1366.

FIG. 41. Winter condition of spore, showing thirteen nuclei in one section. × 857.

FIG. 42. Receptive papilla; oosphere like that shown in *fig. 32.*

PLATE IV. Teratological forms from various species (× 1366 or 857, and slightly reduced in reproduction).

FIG. 43. Antheridial tube penetrating oogonium in which no oosphere has been differentiated; tube branched and heavily coated with pectin; pectin also on oogonial wall in neighborhood of antheridium. *A. Tragopogonis.*

FIG. 44. Oogonium in which no oosphere was developed; antheridial tube small; deposit of pectin on oogonial wall in neighborhood of antheridium; also isolated pectin deposits, presumably in vacuoles; large deposit on the remains of the antheridial tube. *A. Portulacae.*

FIG. 45. An oogonium similar to that shown in *fig. 44;* two antheridia in contact with an oogonium; deposits of pectin lining the walls and projecting into the oogonium in the neighborhood of the antheridium; isolated balls of pectin lying free in the oogonium. *A. Portulacae.*

FIG. 46. An oogonium which developed no oosphere; masses of characteristic pectin distributed through the oogonium; deposits of pectin on the oogonial wall adjacent to the antheridium. *A. Portulacae.*

FIG. 47. Teratological formation of inner wall; redrawn from sketch, slightly diagrammatic. *A. Bliti.*

FIG. 48. Antheridial tube lying against plasmoderma of an oosphere fertilized by another antheridium; oosphere showing five nuclei in this section; antheridial nuclei in dense cytoplasm in the extreme tip of the tube; pectin formation encasing both oosphere and the end of the tube of the supernumerary antheridium. *A. Portulacae.*

FIG. 49. Similar to *fig. 48;* an older condition, showing whole structure surrounded by the remains of oogonial wall. *A. Portulacae.*

FIG. 50. Antheridial tube opening into an oogonium which has developed no oosphere; many male nuclei passing out, tube cut slightly oblique. *A. Portulacae.*

FIG. 51. Two antheridial tubes, each bearing many nuclei, opening simultaneously into one oosphere; one in transverse, one in longitudinal section. *A. Bliti.*

FIG. 52. Oosphere fully differentiated and devoid of nuclei; antheridial tube astray in periplasm; periplasm and antheridium normal. *A. Bliti.*

FIG. 53. An oogonium containing two coenocentra; oosphere bilobed, one coenocentrum lying at the center of each lobe; metaphase similar to *fig. 26. A. Tragopogonis.*

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX.

WILLIAM L. BRAY.

(WITH TWENTY-FOUR TEXT FIGURES)

[*Concluded from p. 217.*]

SEMI-XEROPHYTIC FOREST OF THE HIGH MOUNTAIN SUMMITS AND WATERED CANONS OF TRANS-PECOS TEXAS.—On the higher Guadalupe and Davis mountains the annual rainfall is several inches greater than the normal for that meridian, and greater than in similar altitudes in the mountains of the Great bend of the Rio Grande. The mean temperature also, because of the northerly position and altitude, is enough lower than in other portions of trans-Pecos Texas to make these mountain summits a distinct zone, namely the Transition zone. On these higher summits and in the well-watered cañons leading down from them, the extreme xerophytic conditions of the region are very much modified. This becomes very evident in the aspect of the prevailing formation, an almost mesophytic forest.

The chief elements of the formation are as follows: *Pinus ponderosa*, on Guadalupe peak at 9000 feet, attains a height of 50 feet, with trunk 2 feet in diameter; on the Davis mountains it has yielded clear lumber 18 inches wide. This is the prevalent species, occurring in places in pure formation, as at the "pinery" northeast of Limpio peak. Next in prevalence is *Pseudotsuga taxifolia*, which attains similar dimensions. *Pinus flexilis* reaches a diameter of scarcely more than a foot. Below there begin *Pinus edulis*, *Juniperus pachyphloea*, and the oaks of the xerophytic slopes. The summit formation descends into the upper cañons a short distance.

In addition to the species just cited, the following transition species are important elements: *Cercocarpus parvifolius*, *Ribes viscosissimum*, *Fendlera rupicola*, *Frasera speciosa*, *Geranium caespitosum*, *Campanula rotundifolia*, *Heuchera rubescens*, *Artemisia frigida*, and *Acer grandidentata*. A few of these reach the summits of the highest mountains in the Great bend, but scarcely in force enough to change the strongly upper Sonoran character.

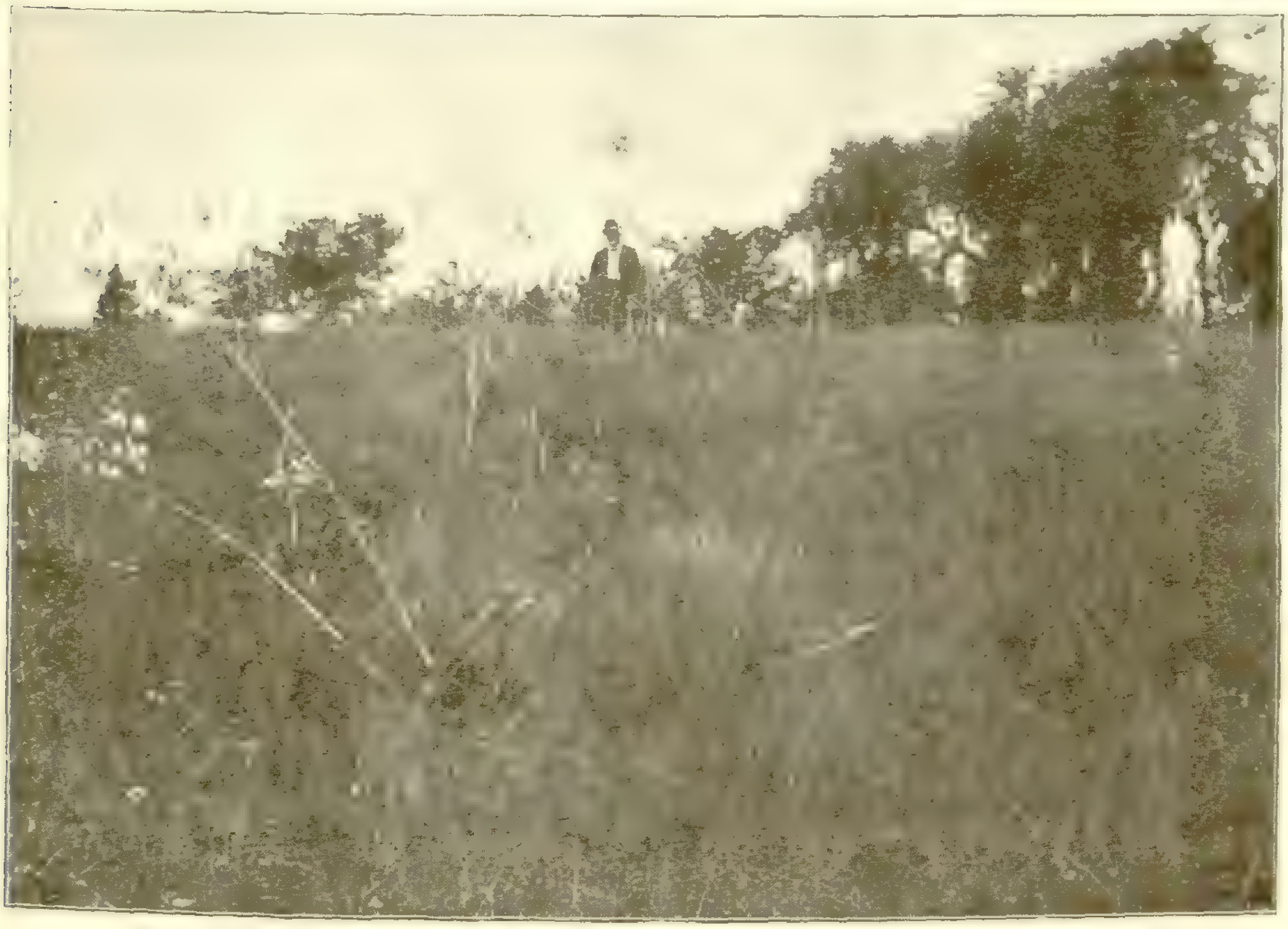

FIG. 14.—Vegetation of adobe slopes and chalk exposures: characteristic of Cretaceous Texas, especially on the Grand prairie and the eastern half of the Edwards plateau.

In the lower cañons, the dwarfed arborescent species of the xerophytic slopes become large trees of regular symmetrical growth. Thus, *Quercus Emoryi* "becomes a straight tree 2 to 4 feet in diameter and 60 feet tall, forming the main feature of the sylva. Here also *Pinus edulis* attains the unusual size of 18 inches in diameter and 40 feet in height" (Havard). These cañons contain in addition numbers of characteristically mesophytic or semi-mesophytic woody species, as species of Prunus, Acer, Philadelphus, and Fendlera, while the sides of watered cañons and the bottoms of dry ones contain those species of the central erosion formation whose range is to the southwest and west. In the main, however, the dry cañons and lower slopes are beset with a chaparral formation, to be discussed separately

XEROPHYTIC AND SEMI-MESOPHYTIC POST OAK FORMATIONS.—The post oak formation furnishes a striking instance of the close relation existing between soil structure and its vegetation covering. Where there are exposures of coarse sand beds and gravelly clays, at least as far west as the 100th meridian, there occurs an arborescent formation whose main elements are the two species of oak *Quercus minor* (post oak) and *Q. Marilandica* (black jack). Very extensive areas of this formation occur also on the western margin of the east Texas forest belt. In the west Texas region the areas are in the main as follows: (1) the extension of Fayette sands into the Rio Grande plain; (2) the gravelly débris and sands of the granitic area and its borders (extending for example westward beyond Fredericksburg); (3) the sands and gravels of the Carboniferous area (Brownwood and Palo Pinto countries); (4) the upper cross timbers (the lower cross timbers to the east of our area are of the same formation); (5) river terrace gravel beds, such as those about Austin.

The character of the formation varies with the underground water conditions. Where the porous textured sand or gravel beds lie so that the soil water level is easily available, the formation is a compact forest with a mixture of semi-mesophytic trees filled in by a lower zone of shrubby species. Such is the character of the formation in the Fredericksburg district and in the upper cross timbers. More frequently, however, the soil water conditions are not so favorable, and as a consequence the formation more nearly reflects the normal climatic conditions, as in the granite country. Then it is no longer a compact forest, but an open timbered grass plain where the trees are of low stature and broad spreading crown, each with the individuality of orchard trees. As a consequence of this open formation, such a forest displays no cooperative capacity in producing a shaded zone, or in collecting humus materials. This leaves a practically continuous grass floor. It also permits the encroachment of sun loving species of the chaparral formations, notably mesquite. Thus many miles of the granite area are covered with a thick growth of mesquite chaparral, with undergrowth of prickly pear and several woody species of the Rio Grande chaparral.

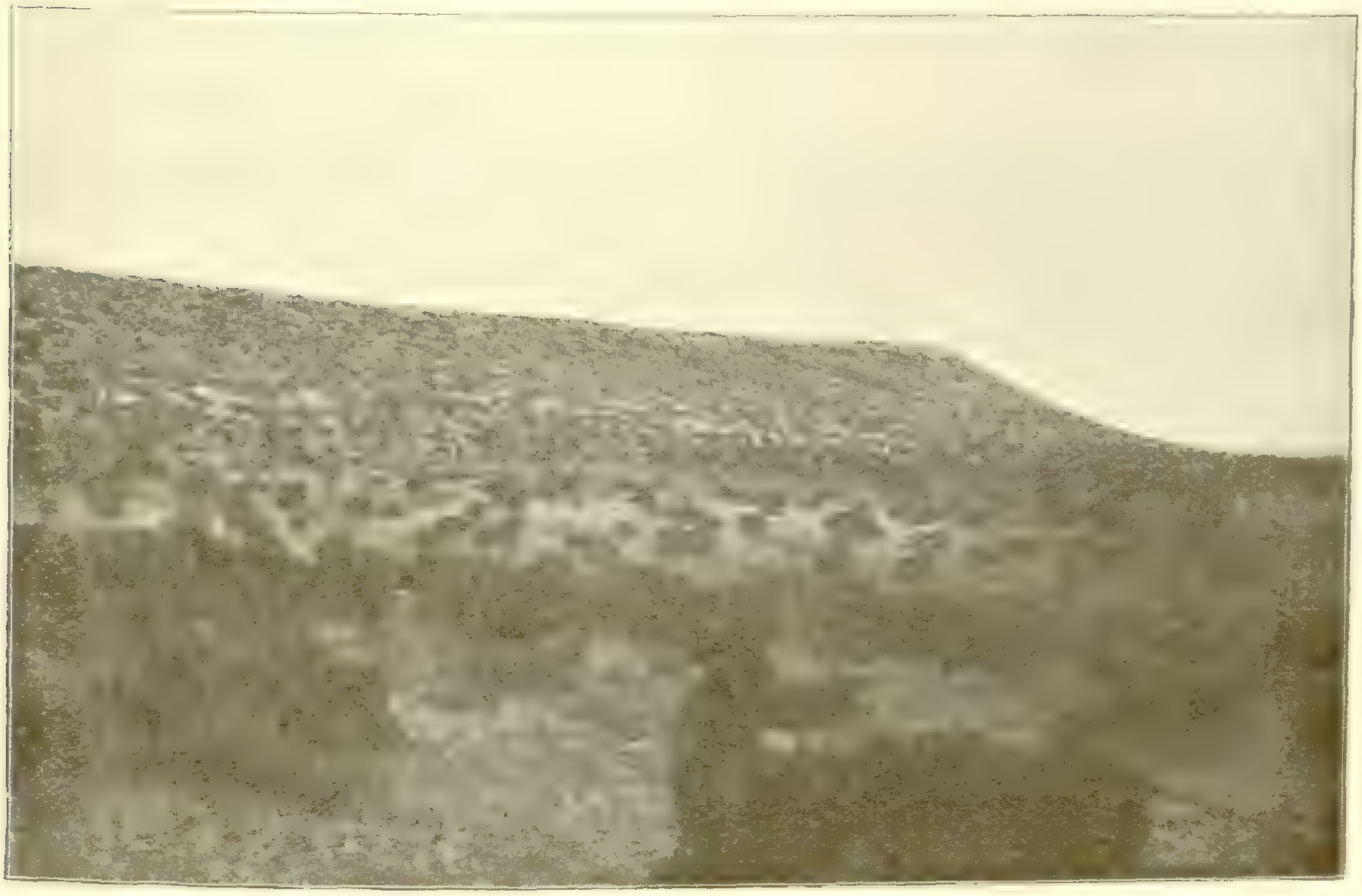

FIG. 15.—*Quercus grisea* and Juniperus formations on an outlying butte of the Staked plains, Big springs; common formation on buttes in western part of central provinces.

The post oak formation of the Rio Grande plain is, as suggested, a southwesterly continuation of the timber of the Fayette prairie sands (in reality of the east Texas forest belt). The southwesterly extension of the formation carries it beyond the Nuéces river, but it has been met by a more vigorous expansion of the Rio Grande chaparral, which has covered the plain as far east as the Guadalupe with a dense mesquite jungle and its accompanying undergrowth of prickly pear.

XEROPHYTIC LIVE OAK FORMATION OF THE OPEN GRASS PLAINS.—That part of Texas lying between the 97th and 100th meridians, that is the transition from mesophytic to xerophytic zones, is often called the live oak belt because of the characteristic occurrence of *Quercus Virginiana*. The live oak formation of the central erosion area has already been described. This is in reality a part of the live oak belt, but the characteristic occurrence of the live oak throughout its zone is upon the open grass plains of the central region from the Gulf to Red river.

It occurs in so open and irregular a manner as barely to deserve the name of formation. It is in reality a punctuating feature in a pure grass plain formation. The occurrence is in small isolated clumps whose ecology is that during the first years of growth a successful struggle against grazing animals and other encroaching agencies is best waged from these compact masses, which themselves come to have the form of crown and individuality of a single tree. These clumps may be called centers of infection, for by them the species is spreading. Some exceptions to the very open formation occur, as in Live Oak and Bee counties, where the live oak timber becomes a very prominent feature of the landscape.

The species in this zone is very hardy, and attains a great age and large growth. The characteristic growth is expressed in the following dimensions, which though far above the average as to actual size are by no means unusual; diameter of trunk four feet; height of trunk to main branches six to eight feet; total height of tree thirty to forty feet; spread of crown one hundred feet.

MESOPHYTIC FOREST FORMATIONS OF THE STREAMWAYS.—There are two general types of this formation, namely that of the open streamways or broader alluvial river valleys, and that of the enclosed box cañons of the erosion areas.

Timber formations of open streamways.— It happens that, excepting the Rio Grande and Nuéces, the larger rivers rise in regions of very low rainfall, and lead into zones of greater (often heavy) rainfall. It happens, also, that the direction of flow brings them within or accessible to the east Texas forest belt. The result is that the streamways are lines along which some elements of the forest belt spread into regions far beyond its normal boundaries. Thus, the Red river, Trinity, and Brazos carry purely mesophytic forests to the 97th meridian, and heavy timber far into the central province; and the Colorado, aside from the timber of its cañon course, carries big growths of pecan and sycamore beyond the 101st meridian.

Floristically the streamway formation does not include the species which give the east Texas forest its distinctive character. The pines, gums, magnolia, maple, and water oaks are not present, but on the contrary a selected group of species, which more readily adapt themselves to conditions of the open country, greater exposure to dry winds, greater sunlight, and less available water supply. Such are the hackberry, pecan, sycamore, elms, and some oaks. These species are constant associates in the streamway timber of the prairies. Farther out on the plains, toward the headwaters of the rivers, after the streamway timber above described has ended, the plains cottonwood occurs in its characteristic "groves" about basin springs, as, for example, at Big springs, and in similar places in trans-Pecos Texas.

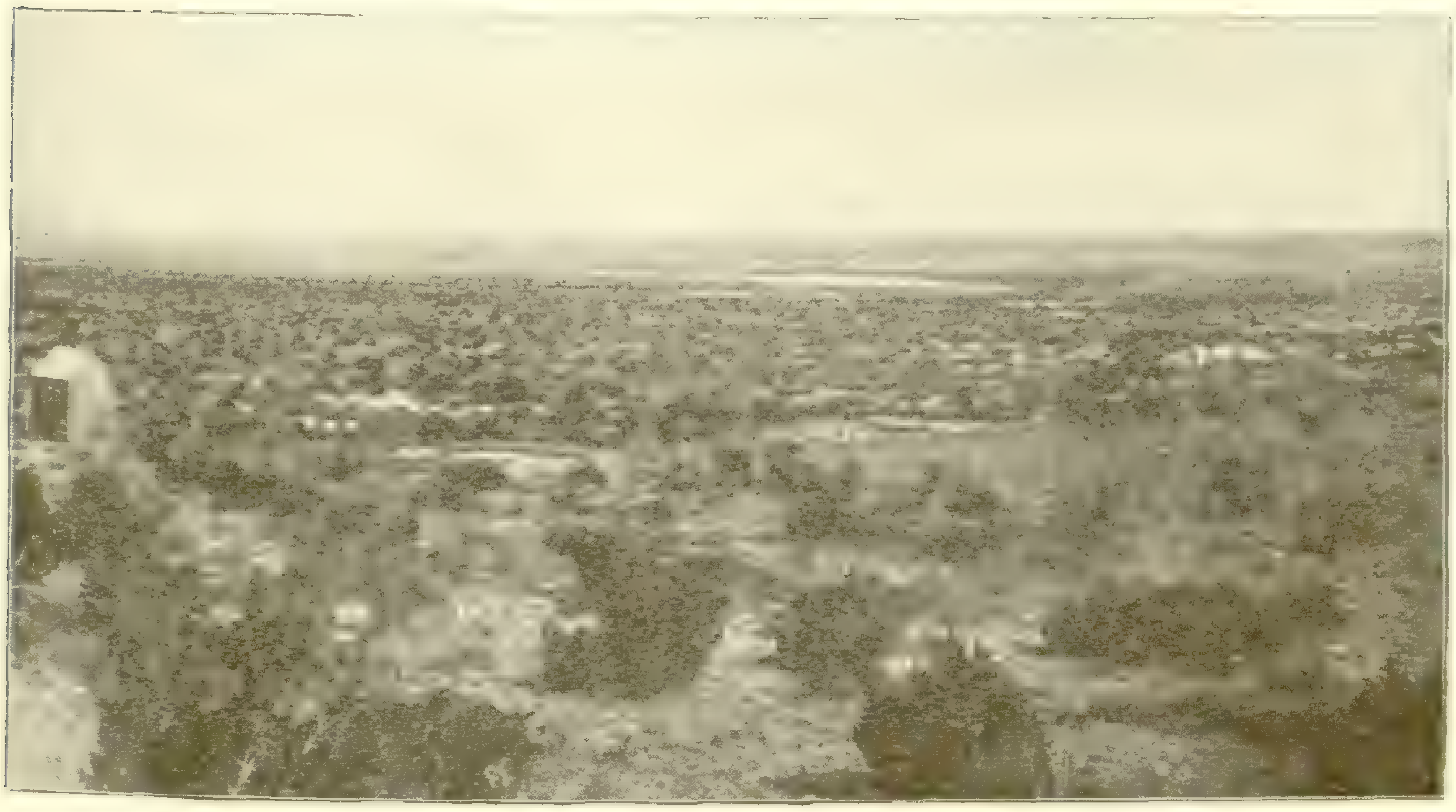

FIG. 16.—Chaparral formation on Staked plains débris, Big springs; a northeastern extension of the trans-Pecos Sonoran chaparral belt.

The Nuéces river, notwithstanding its course through the semi-arid Rio Grande plain, and its distance westward from continuous forest areas (below its cañon), is accompanied by a narrow belt of mesophytic timber of which the largest growths are the species just cited for the other streamways. Other species from the southwest, habitually only shrubs, here become small trees.

The timber of the Rio Grande valley presents three types of formation. The first is the cottonwood-willow association above the Grand cañon, with the Texas green ash (*Fraxinus Berlandieriana*), and two or three minor species in the side cañons of the Great bend. In the heavily timbered Cibolo cañon, for example, Havard reported *Populus Fremontii* four to five feet in diameter, and Texas green ash forty to fifty feet high and one to two feet in diameter. The second type, which is mainly that of the river valleys of the Nuéces and other rivers eastward, occupies the middle course of the Rio Grande below Eagle pass, but is at best a very insignificant feature. The third type occupies the valley below Rio Grande city. This is a mixture of eastern river valley species with species of the warmer Mexican region, as *Ehretia elliptica*, *Bumelia lycioides*, and several Mimoseae which have here become fair sized trees. The tropical affinities are finally marked in the lower course of the river by the appearance of an open formation of *Sabal Mexicana*, a tree twenty to thirty feet high.

Timber formations of the box cañons.—Streams which rise in or cut across the central erosion area of the Edwards plateau have worn deep and narrow channels known as box cañons, which in many cases are so sheltered and well-watered as to furnish proper conditions for typical mesophytic vegetation. Such cañons, for example, are those of the Guadalupe system and the Perdenales. The woody vegetation in these cañons, as well as the herbaceous, is that of the interior margin of the Atlantic coast plain, and yet it is to be noted how isolated these cañons are with respect to the mesophytic regions of the coast plain. In the Turtle creek cañon in Kerr county sixteen species of trees and shrubs were found which are not a part of the typical xerophytic woody vegetation of the region, but are the commonest elements of the Atlantic coast plain forests. Herbaceous species like Ranunculus, Aquilegia, Botrychium, and Dryopteris were naturally associated in this formation. The timber growth attains large dimensions in some of these cañons. On the Guadalupe at Kerrville a cypress stump (*Taxodium distichum*) was found measuring over four feet in diameter.

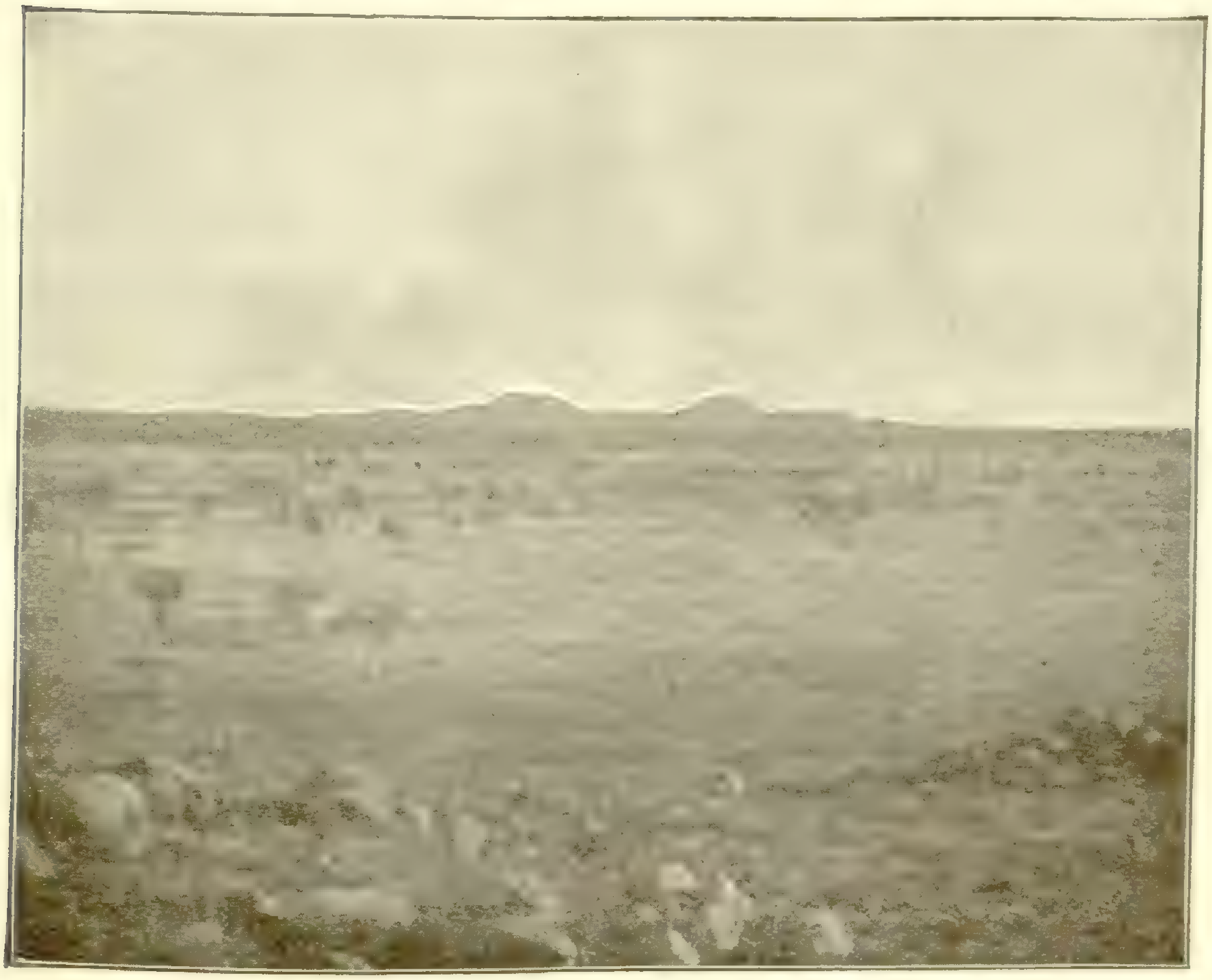

FIG. 17.—A red beds prairie, central province; the spread of mesquite is shown.—From Hill's Phys. Geog. Texas.

Mention has already been made of the mesophytic cañon timber of trans-Pecos Texas in connection with high mountain forests and the Rio Grande cottonwood-willow and ash timber. These cañons also furnish shelter for a few semitropical, mostly xerophytic, species common to the lower Rio Grande.

CHAPARRAL FORMATIONS.

The term chaparral as here employed is designed to carry with it not merely the idea of a shrubby formation as opposed to an arborescent one, but also a formation occupying a specific relation to ecological factors. It is a woody vegetation of warm temperate or semi-tropical requirements; adjusted to hydrometeoric conditions wherein there is a minimum of rainfall, a dry air subject to regularly recurring movements of great velocity, and a high percentage of days of intense sunshine; related to edaphic factors in which the soil (waiving its possible great fertility or the fact that it may have had a flood débris origin) has the loose, shifting, uncohesive quality of soils formed by dry weathering and destitute of vegetable mould, if not gravelly or stony: and where the soil water level is too deep to be available for any but perennial plants with far reaching roots. Such conditions of course dwarf the growth of any woody plant subjected to them, even if it could endure them at all. Chaparral is the product of such conditions, and while characteristically shrubby, many species may under other conditions attain to arborescent size, never of course becoming large trees.

There are two general types of chaparral formation in the West Texas region, differing both floristically and ecologically. One is the chaparral of the Rio Grande plain, the other that of the trans-Pecos region. The difference between these two formations is due primarily to the climatic differences between the two provinces, and secondarily to differences in geologic and physiographic conditions.

THE RIO GRANDE CHAPARRAL.—This formation is typically a low, more or less impenetrable bush vegetation, covering continuously vast areas, and varying in height from two or three feet to ten or fifteen, according to varying ecological conditions. In the former case, the habitually shrubby and more xerophytic species prevail, for example within twenty miles of the Rio Grande from Del Rio to Laredo; in the latter, the larger species of Mimoseae form the main body of the formation, notably *Prosopis juliflora* as found from San Antonio to Kenedy. No fewer than forty species associate in this formation, in many cases a limited area being tolerably uniformly covered by at least half of all the species (*figs. 7–10*). On the other hand, a single species constitutes almost the entire formation over extensive tracts.

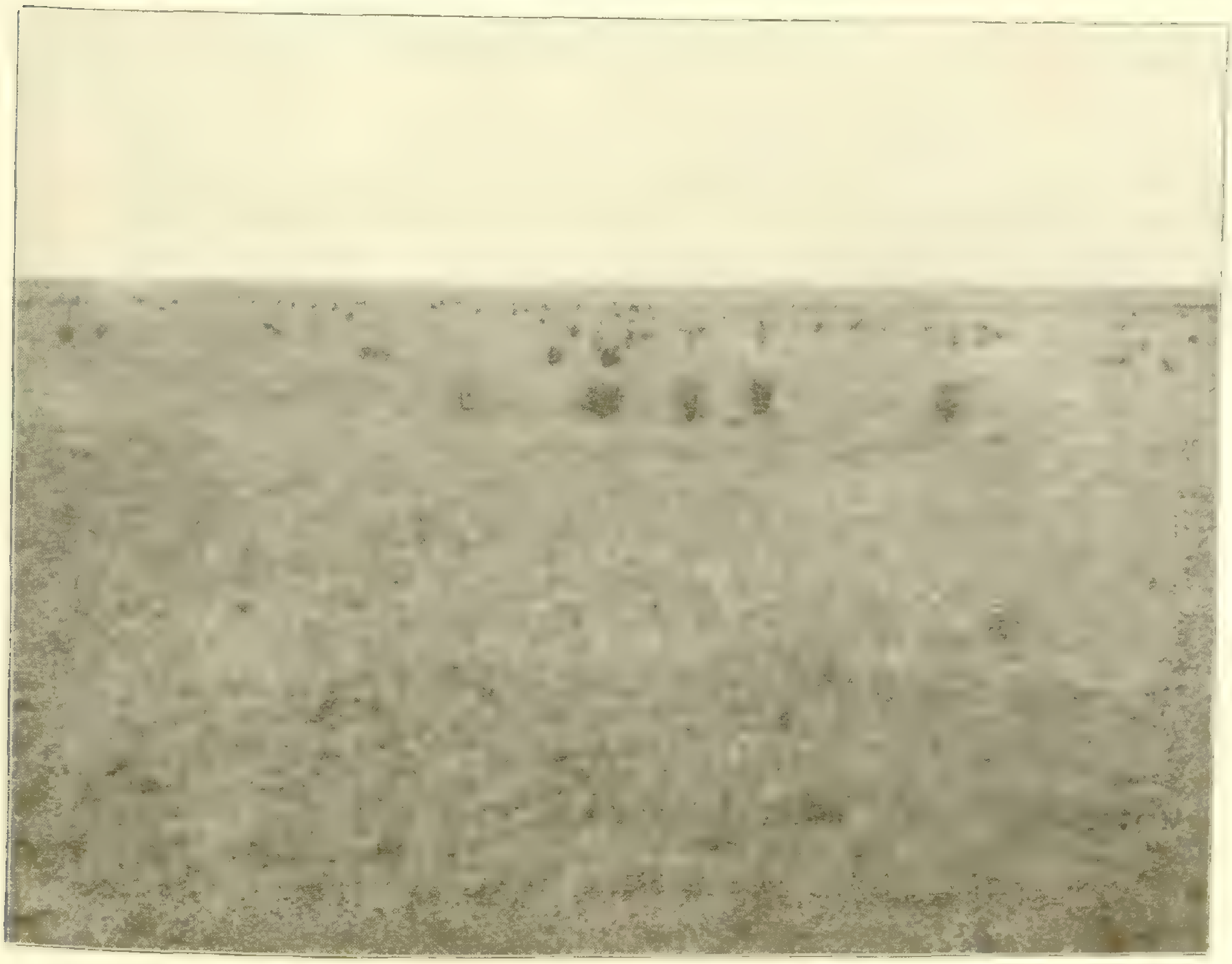

FIG. 18.—Summit of the Staked plains, 3,700 ft. alt.; grass formation with *Yucca glauca*. Branched inflorescence = Y. constricta in fruit.

On the basis of temperature, there is a distinction of species into those of semitropical and even tropical affinities and those able to endure the freezing winter temperatures of the warm temperate zone. The former occur chiefly in the lower Rio Grande country, the latter constitute the chaparral of the northern half of the plain, spreading also by some species into central Texas. Geological structure and conditions of soil act powerfully to determine the *facies* of the formation upon any given area. Thus, gravelly slopes, denuded of finer sediment, may have a pure formation of straggling *Parkinsonia Texana*, and basalt ridges are thickly covered by a short bushy formation of *Acacia Berlandieri*. The prevalence of Mimoseae and Caesalpineae in the Rio Grande chaparral deserves special mention. No less than 30 per cent. of the number of species and a far higher percentage of actual individuals would represent the strength of these elements in the formation. This also emphasizes the semitropical affinities of the formation. The condition now prevalent in the Rio Grande province represents a state of unstable equilibrium between chaparral and grass formations (*fig. 8*). These conditions are of a nature to favor the encroachment of the chaparral. This interesting phenomenon is discussed elsewhere in this paper.

Coming next to consider individual features of the chaparral, certain conspicuous types are of special prominence.

Prosopis juliflora or mesquite formation.—In the Rio Grande plain this occupies the level areas of fine compact silty débris. Similar "mesquite flats," as they are commonly called, are found in similar situations throughout the lower Sonoran area in Texas, but the species also occupies black prairie soils in some areas. The most massive formation of mesquite occurs on the silty débris plains on the northeastern border of the Rio Grande plain near San Antonio. From thence southeastward the country is a vast mesquite forest some fifty years old and fifteen to twenty feet tall. In the lower Rio Grande valley individual trees attain (for this species) gigantic size, reaching two feet in diameter and thirty-five feet in height.

Acacia Farnesiana or huisache formation.—This prevails especially on the low moister coast prairie clays. The species is more limited than the mesquite in both moisture and temperature requirements. Its spread has been on the coast prairie as far east as Galveston. Although cultivated as far inland as at Austin, its natural spread is not much beyond the coast country and the lower Rio Grande.

Acacia amentacea formation.—This formation is the prevalent one in the northern half of the Rio Grande province. It is the "black chaparral," whose foliage and beans yield tons of forage. It constitutes 60 to 75 per cent. of the shrubby vegetation on many thousands of acres in Maverick, Dimmitt, and Webb counties (*fig. 9.*)

Acacia Wrightii formation.—This is known as "bee blossom," and "cats claw," and is especially prevalent in the northern part of the province between the Nuéces and Medina rivers. Generally it is an open formation on grass plains, and is frequently of low arborescent dimensions.

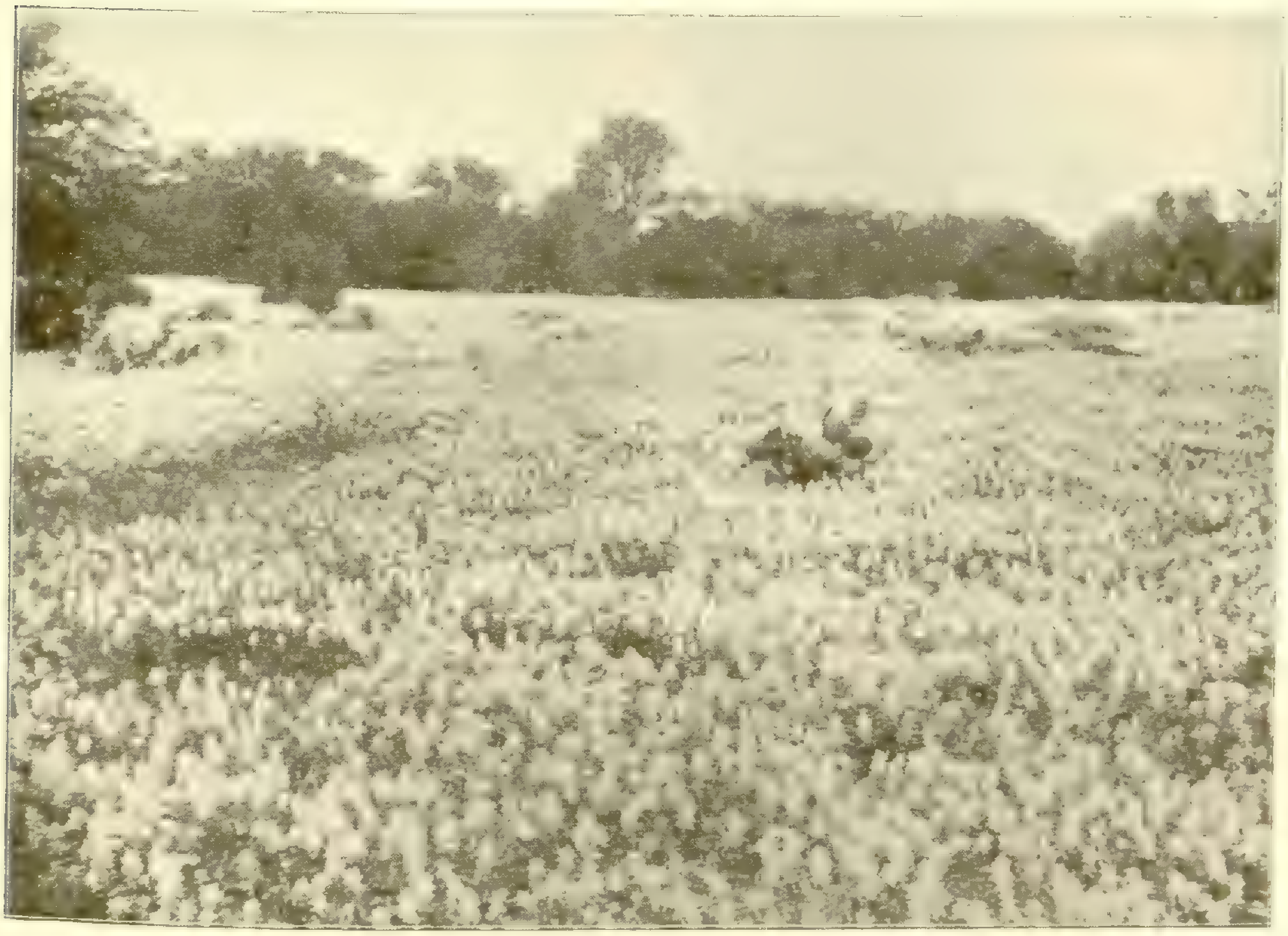

FIG. 19.—Pure formation of *Lupinus subcarnosus* at Austin; a type of prairie annual.

Acacia Berlandieri or huajillo formation.—This is a very striking vegetation occupying the basalt ridges and cones extending east and west along the northern border of the province. Farther southeast the formation has been noted on coarse gravelly ridges denuded of finer sediment. Everywhere its height scarcely exceeds three or four feet.

Parkinsonia Texana formation.—The coarse gravelly débris slopes in the Eagle pass quarter of the province are occupied by this species. It is an habitually procumbent or straggling and spreading shrub which, while occupying the ground fully, is a very diffuse covering.

Leucophyllum Texanum formation.—This species occurs in solid mass in the more arid parts of the province, especially within twenty miles of the Rio Grande on both the Texan and Mexican sides. The hairy felt covering of the foliage gives it a light tone which is very striking to the eye.

Opuntia Lindheimeri formation.—As an ecological type it is scarcely consistent to class this succulent with dwarf lignescent vegetation, and as such a type it is discussed elsewhere (see under "succulent vegetation"). But the "prickly pear" is so thoroughly a part of the bush vegetation of the Rio Grande country as to necessitate its mention here. The association of this species with mesquite has been remarked. Together they have preempted a vast amount of territory, and have introduced economic problems of no small concern, as well as interesting ecological phenomena.

On the upper course of the Rio Grande, within the Rio Grande plain, the chaparral formation assumes a more xerophytic aspect, and species of the trans-Pecos chaparral appear. A transverse section across the Rio Grande embayment from northeast to southwest would encounter this same transition to the extreme xerophytic type on the Mexican side, where the central plateau and sierra region begins, that is, at the outer rim of the embayment.

THE TRANS-PECOS CHAPARRAL.—The area covered by this type of chaparral embraces, besides trans-Pecos Texas, the north Mexican plateau and the arid lower Sonoran zone plateaus of New Mexico, Arizona, and southern California. Its northeastern extension includes the western part of the Edwards plateau and the southern slope of the Staked plains.

In the trans-Pecos region the formation occupies the cañon sides and bluffs from the Pecos westward, the rougher southern end of the Stockton plateau, the lower slopes and foothills, the arid mountain slopes (especially in the Great bend), the dry cañons of the Great bend region, and the bolson deserts. On the whole it is more of a rock vegetation than the Rio Grande chaparral, but it also occupies the finer débris-covered slopes and bolson plains.

Compared with the Rio Grande chaparral it is in large measure floristically different. Where it contains the same species, as for example *Prosopis juliflora*, the habit is very different, being in this case dwarfed and shrubby bushes, while in the Rio Grande plain it is habitually low arborescent. The Mimoseae and Caesalpineae form less than 10 per cent. of the species, individuals occur less abundantly, and, excepting *Prosopis juliflora*, are different species from those of the Rio Grande plain. A more striking individuality as ecological types is attained in the species of this formation. This is seen in the greater abundance of the Ephedra type, the felt-covered Eurotia and Croton type, those impregnated with volatile resins, like Larrea and Flourensia, and the wand-like, fluted, thorny stems of Fouquiera (*fig. 20*).

About thirty species are recognized as more or less prominent constituents of chaparral formation of the trans-Pecos Texas. Apparently not so great a percentage of these species associate on any one area to constitute the formation, though the number of species occurring, for example, on the sides and bluff of the Pecos cañon would be little less than half the total. Considering types of the trans-Pecos chaparral formation in detail, it must suffice to point out the following.

Larrea Mexicana or Mexican greasewood formation.—This is by far the most notable formation of any single species. It is especially characteristic of high gravelly mesas (as about Fort Bliss, El Paso), and of the bolson deserts, extending even to highly charged alkaline soils at the center of such basins (*fig. 21*). This greasewood formation is composed of such regular open growth as to appear like plantations. The plant is a shrub with spreading top, averaging less than three feet tall. Its special

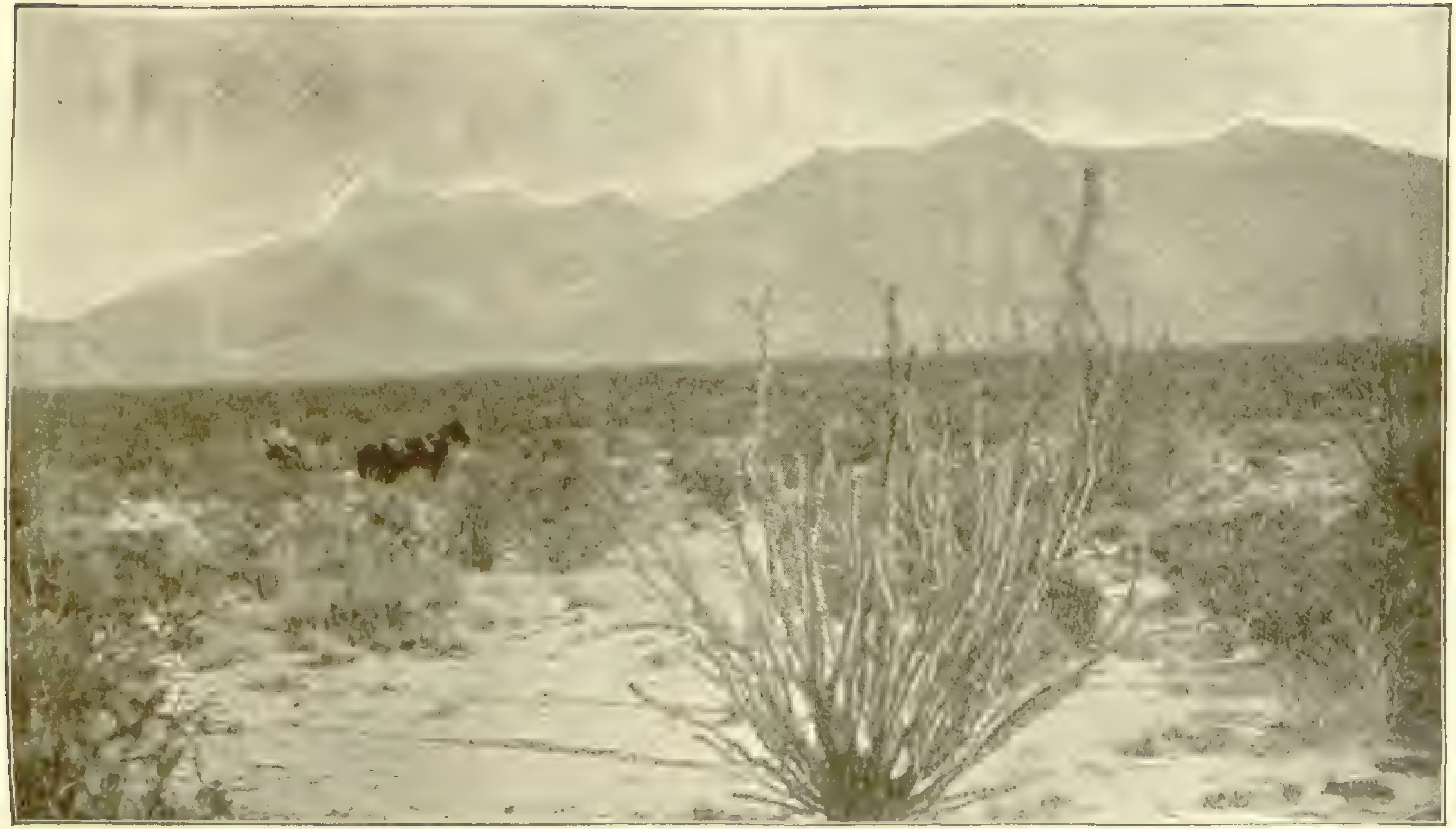

FIG. 20.—Chaparral formation on desert basin southwest of Sierra Blanca Quitman mountains; *Fouquiera splendens* in the foreground.—From Hill's Phys. Geog. Texas.

adaptation seems to lie in the great quantity of resinous matter in the leaves. The odor from this gives notice of the nearness of a greasewood formation.

THE TRANS-PECOS TYPE OF CHAPARRAL EAST OF THE PECOS.—As already noted, this chaparral spreads east of the Pecos upon the western margin of the Edwards plateau, especially its plains area, and upon the southern border of the Staked plains. The easterly extension of the more arid lower Sonoran area is indicated in this chaparral. A typical case may be cited in the vicinity of Big springs in Howard county (*fig. 16*). This is a region covered by the plains débris. The arid mesas are covered by a characteristic formation of chaparral in which not less than twenty species occur, among which are more than 50 per cent. of the characteristic trans-Pecos species.

THE RIO GRANDE CHAPARRAL IN CENTRAL TEXAS.—The chaparral of the Rio Grande plain terminates abruptly at the foot of the Balcones escarpment, where the xerophytic forest of the erosion area begins. A few species, however, mingle with the timber species, and occasionally (as in the case of *Condalia obovata*, *Zizyphus obtusifolia*, and others) forms a characteristic chaparral bush or thicket. On the grass plains of the granite country a much more pronounced encroachment of woody vegetation is taking place. As already pointed out, the mesquite has spread over most of the province. With it have gone the prickly pear and several shrubby species which together are building up a compact chaparral formation. The Rio Grande Mimoseae, except Prosopis, and Caesalpineae, and all others of the more characteristic species, do not appear in this chaparral.

FORMATIONS OF SUCCULENT OR WATER-STORAGE VEGETATION.

This third general type of formation stands out in strong contrast with the two preceding types of grass and woody vegetation. The contrast lies in the fact that whereas the preceding types have adjusted themselves to xerophytic conditions by retaining the least amount of sap-bearing tissue, this type has gone exactly to the opposite extreme. The areas occupied by formations of this type are also in the main different from those of the other two. With few exceptions, this latter might be designated as a kind of rock vegetation, for the most significant elements are constantly associated with high, arid, stony slopes. As an ecological type the succulent vegetation is to be regarded as a more efficient adaptation to extreme aridity than the grass or woody vegetation. Consequently, it is to be found in its most typical display in the arid regions of trans-Pecos Texas.

In this discussion little account can be taken of the numerous ephemeral species like those of Sedum, Talinum, Portulaca, and others, but the consideration is particularly given to those more evident as features in the landscape. Of the elements composing this more conspicuous vegetation, there are three types, each forming a distinct and close genetic group. These are the Cactaceae, the Yucceae, and the Agaveae. A brief consideration of these may precede the discussion of the three types as associated in a single formation.

THE CACTUS VEGETATION.

A rather general survey of this group gives three types, each associated with a distinct physiographic feature: (1) the flat-jointed opuntias of the Rio Grande plain and central Texas; (2) the woody cylindrical-stemmed opuntias of the high plateau plains; and (3) the cylindrical and spherical cacti of arid stony slopes.

Opuntia Lindheimeri formation.—The prevalence of this formation in the Rio Grande plain has already been noted in discussing chaparral vegetation. The species here considered has spread beyond the Rio Grande plain to the north and east beyond the Colorado. To the east and southeast of Austin there are some extensive and typical prickly pear fields. It is present with the mesquite in the granite country in great abundance. In the Rio Grande plain the quantity of vegetation formed by this species is of almost incredible bulk. The level silty débris plains are its common habitat, but stunted formations of it also occur on arid gravelly soils, and on chalk soils about Austin. In the valley of the Nuéces river, about midway of the plain, this Opuntia attains gigantic size, being said to exceed a height of ten feet. In the vast mesquite forest on the northeastern border of the Rio Grande country, the prickly pear is an undergowth four or five feet high. These two species together are practically blocking up large tracts of pasture lands, not only changing grazing conditions, but rendering the use of such lands for agricultural purposes an expensive enterprise. This Opuntia fruits regularly and in great quantity, and apparently is chiefly spread by means of seeds. These have been found germinating in great numbers in cow chips. The juicy fruits are eaten not only by cattle, but evidently by other mammals as well, and by birds.

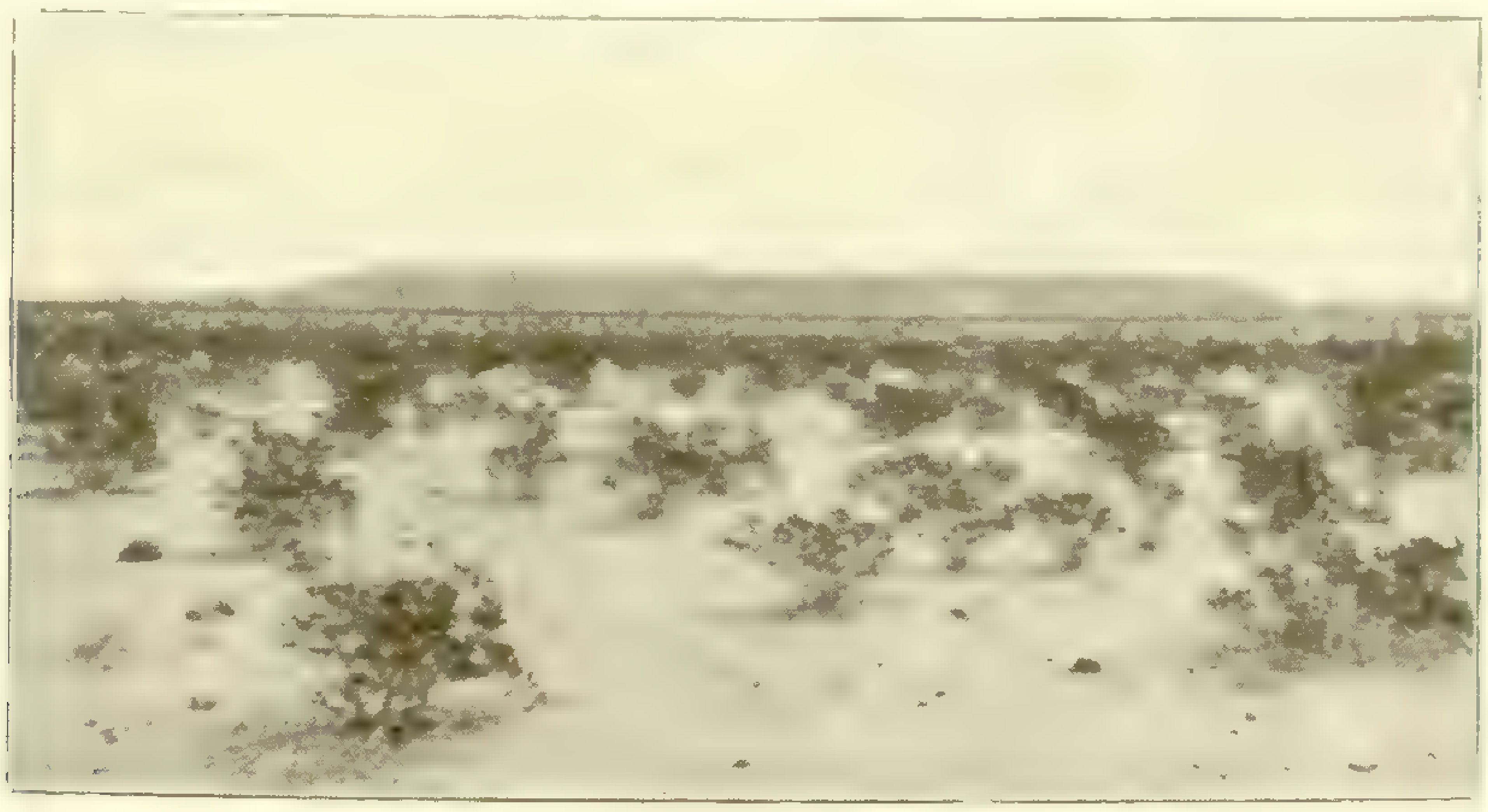

FIG. 21.—*Larrea Mexicana* (Mexican greasewood) formation; typical bolson desert of trans-Pecos Texas; *Fouquiera splendens* associated here.—Kodak view by R. T. Hill.

THE CYLINDRICAL OPUNTIAS.—These are chiefly plants of the high plains westward, *Opuntia frutescens* being an exception. This species is part of the chaparral of the Rio Grande plain and the adjacent provinces northward. It occurs especially in association with spreading shrubby species by which it partially supports its slender stems, and together forming well-defended clumps of chaparral, from which there is a gradual encroachment upon the grass formation. The presence of the Opuntia prevents the shrubs from being eaten back by cattle. *Opuntia arborescens* is conspicuous on the high grass plains of the Stockton plateau and westward. It also occurs east of the Pecos at the foot of the Staked plains, and to a less degree on the summit of the south half of the plains. At the base of the plains in Borden county it is very common and of large size, reaching seven and eight feet in height. This Opuntia does not occur as a continuous formation, but at intervals serving rather to punctuate the grassy landscape. This is always noted by travelers who observe the landscape of the trans-Pecos grass plains traversed by the railways.

THE BROAD CYLINDRICAL AND SPHERICAL CACTI occur upon arid stony slopes of trans-Pecos Texas as the most extreme type. These associate with Agaveae and Yucceae to make the type of formation to be discussed subsequently. East of the Pecos, on stony hillsides, rock bluffs, and even on coarser gravel ridges, cespitose species of Cereus occur, often (as in the case of *C. caespitosus*) forming patches from a few yards to many rods in diameter, as on broken granite slopes in Llano county.

THE YUCCA VEGETATION.

The prominent yucca vegetation of the so-called "yucca belts" is a part of a mixed formation to be considered presently. Independently of this, certain areas of yucca vegetation are to be noted (*fig. 24*). First, the occurrence of *Yucca Treculeana* in the lower Rio Grande and Gulf coast region, where it is said to form "open stunted forests." Again on the cañon sides in the central erosion area the same species (apparently) forms a conspicuous feature of the cañon flora. Second, the constant occurrence of *Yucca rupicola* upon the talus débris of slopes leading down from crumbling limestone formations. The formation, of which this is but an element, is one of the most distinct minor formations of the cretaceous areas east of the Pecos. Third, *Yucca angustifolia* is particularly characteristic of the Staked plains region. Here it follows the gentle slopes about shallow basins or the wave-like undulations where the soil is looser and more sandy. Fourth, Nolina formations on the Rio Grande plain below the Balcones escarpment, and at many places on stony slopes as far east as the Colorado. The great tufts of this so-called bunch grass form the most conspicuous vegetation on the finer débris below the yucca belt in the Rio Grande plain.

THE AGAVE VEGETATION.

In addition to species of the Agaveae which associate in the mixed cactus-yucca-agave formation to be next described, two species require notice. *Agave Wislizeni,* or "Texas mescal," is a mountain species (apparently upper Sonoran to Transition) occurring (according to Dr. Havard) in all the mountains of western Texas, and formerly much used for food, beverage, and medicine. *Agave Americana*, or "Mexican maguey," enters the Texas region in the lower Rio Grande plain, and two or three more insignificant species are also present.

MIXED CACTUS, YUCCA, AND AGAVE FORMATION OF ARID STONY SLOPES.

While the trans-Pecos region possesses more or less of each of the three types included in the above named formation, in most of its physiographic provinces a little investigation shows that in the main the three are found upon one type of physiographic structure, either more or less equally represented, or one type predominating. In traversing the high grass plains of the Stockton plateau and westward it is noticed that in approaching the crest of one of the broad undulations, or any relief feature notably above the plains level, a unique yucca vegetation sets in, to be followed again presently by other stretches of grass plain. Where the margin of the plain rises up into the bordering foothills, there again is the yucca vegetation. Again, on the rim of the enclosed bolson basins this formation is present, and finally on many of the gentler slopes of the mountains (especially those with timberless arid slopes) the yucca vegetation is present as the chief vegetation feature. This is the apparent condition seen at a distance, and sometimes the Yucceae are alone in the formation. But a nearer look commonly reveals the less conspicuous cactus and agave members of the association (*fig. 22*). In all the physiographic features cited, practically the same

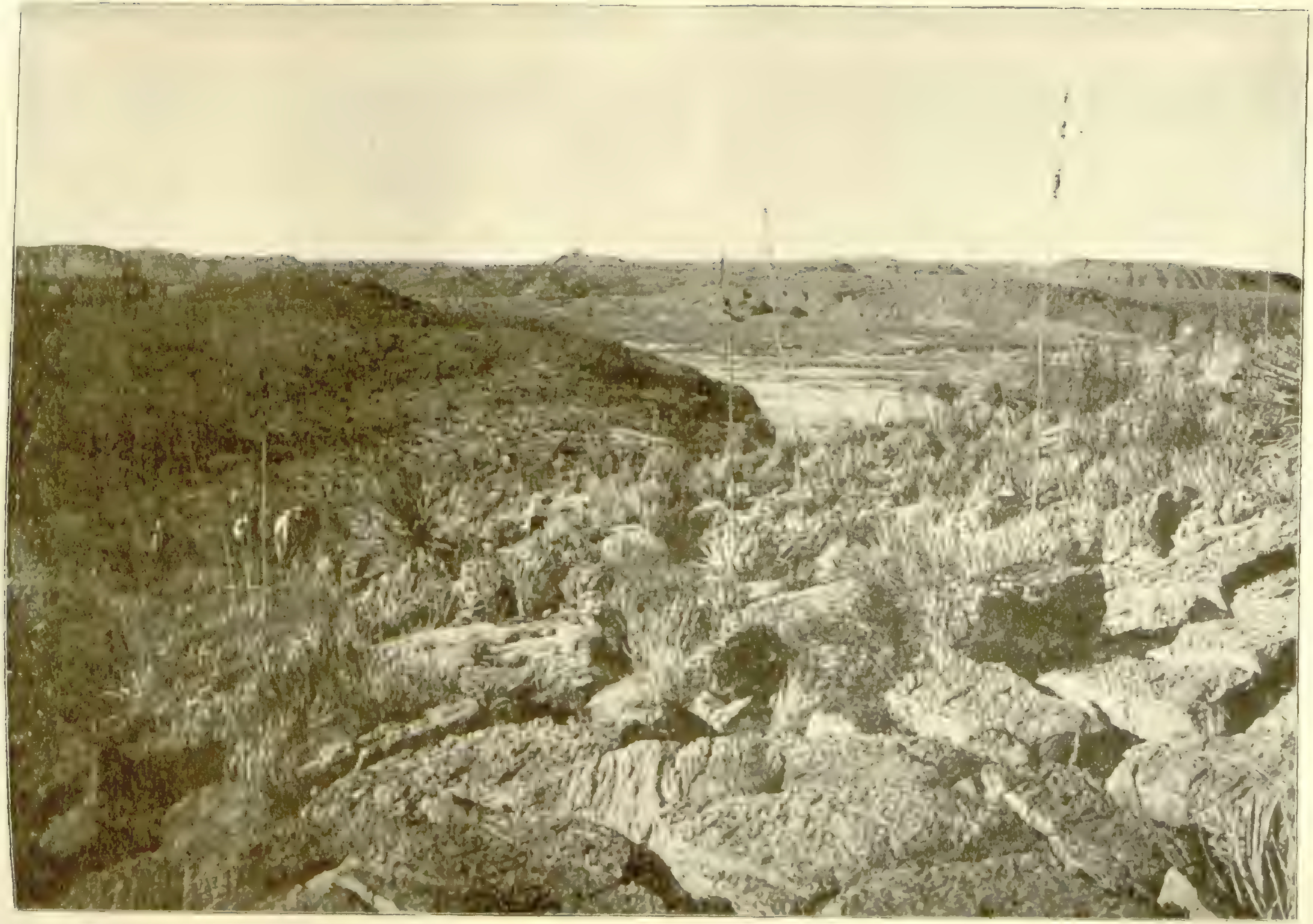

FIG. 22.—Yucca-agave-cactus formation of stony slopes; mountains of the Great bend of the Rio Grande, in trans-Pecos Texas.—Photograph by R. T. Hill.

ecological conditions prevail. In the wearing away of the mountains in this dry climate the débris is carried downward to fill the intervening basins. The finer débris being carried nearest the basin center, on the slopes at the outer rim of the basin lies the coarser débris, an unconformable mass of coarser or finer stony talus. This talus débris may extend far up the slopes of mountains, which receive but a few inches of rainfall annually, especially those in the Great bend, and thus carry the formation of cactus, yucca, and agave with it. These "yucca belts," as Mr. Hill calls them, when projected upon a map appear as marginal lines of basins and to encircle the various mass elevations. The formation extends even to the east of the Pecos cañon along the coarse débris from the Balcones escarpment. The abundant occurrence of *Yucca Treculeana* and several species of cacti on the timberless cañon sides as far east as the Colorado may be regarded as an extension of the same formation.

As to the prominence of the several types in the formation, as already stated, viewed from a distance the yucca vegetation seems the only prominent one. It is in reality so only in some instances. In other cases other types play the chief rôle, so that several variations exist, as illustrated by the following:

Open forest-like formations of the palmo or Yucca macrocarpa.—This largest of our yuccas is very abundant in the Great bend region, covering the long arid slopes with an open formation of yucca trees "with caudex ten to twenty feet high and one to two feet in diameter" (Havard).

Lechuguilla (*Agave heteracantha*) *and sotol* (*Dasylirion Texanum*) *formation.*—This is a very characteristic formation of very rough stony slopes in which the lechuguilla forms a most obnoxious feature because of its agressive short bayonet-like leaves. This formation is very common as far east as the Nuéces cañon.

Formations in which globular and cylindrical cacti predominate.—These include several species of Mamillaria (among them forms called "devils pin cushion"), Cereus (notably the strawberry cactus, *C. stramineus*), Echinocactus (especially the "Turk's head," *E. longihamatus*), and Anhalonium. Such formations indicate about the ultimate point of extreme exposure to intense light, burning midday and chilling midnight temperatures, and moistureless air and soil.

There is still another and very striking species associated with the cactus-yucca-agave formation, especially on the most arid stony mesas and slopes where cacti predominate. This is *Fouquiera splendens.* Its slender, thorny, wand-like stems arise in small groups from the surface of the ground to the height of five to eight feet, bearing leaves only in a tuft at the apex. It is as if the most arid spots had been located and marked out by this plant (*fig. 20*).

ROCK VEGETATION OF CRYPTOGAMOUS PLANTS.

The formation of succulent vegetation might be designated, on the whole, rock vegetation, occurring as it does either upon stony talus or on cañon bluffs. Certainly many succulents not mentioned in the discussion are characteristic rock plants, but the attempt here is to select types of formation which in a peculiar or conspicuous way constitute the characteristic vegetation. The xerophytic cryptogamous plants constitute such a vegetation. They are a rock vegetation either because they occur upon a bare rock substratum or because they inhabit clefts or fissures in the rocks, or dry rock ledges. The former play an important rôle in disintegrating solid rock, as the granitic lichens, or in promoting the accumulation of a matrix of organic material upon barren surfaces, as the Cyanophyceae on bare chalk or compact limestone débris. Throughout the central Texas Cretaceous areas the occurrence of these low plants is very noteworthy. They consist of a species of Nostoc which occurs in curled, crumpled masses after rains or foggy weather, literally covering the ground; a mat-forming Scytonema; and several matted, leathery lichens.

The so-called rock ferns are ecologically the most noteworthy elements of the vegetation of rock fissures and ledges. The several genera and numerous species of ferns constituting this xerophytic group are associated with the Sonoran climatic

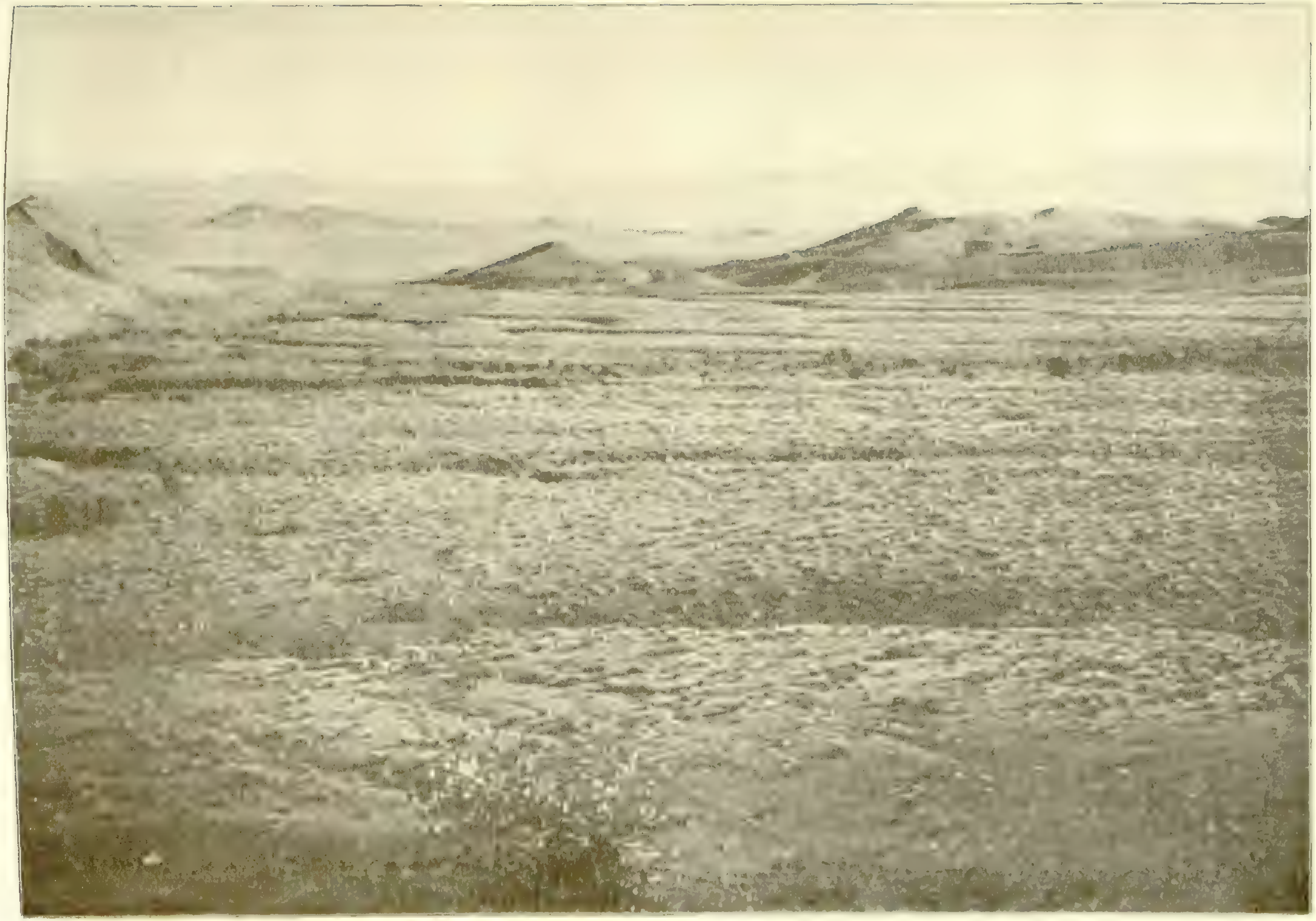

FIG. 23.—A dead "bunch-grass" desert, adobe soil; Tomillo desert, trans-Pecos Texas.—Photograph by R. T. Hill.

conditions of the southwest, and occur not only throughout that area, but over its southward extension along the continental axis south of the equator. Their distribution in the west Texas region coincides with the areas of escarpment, and of cañon erosion. They occur, for example, throughout the central erosion area. Aside from the various means of adapting the vegetative plant to xerophytic conditions, the ecological relations of this group of ferns has not been much studied.

Two additional important species are to be noted, namely, *Selaginella lepidophylla* (a "resurrection" plant) of the trans-Pecos region, but also extending eastward on limestone bluffs and knobs to the Frio river; and *Selaginella rupestris* (the forms still so designated) is especially abundant in the granite area, but it appears to be in all of the mountainous or hilly areas of west Texas (on dry gravel ridges at Austin), on limestone hills on the upper Nuéces cañon, and in trans-Pecos mountains. Several extremely xerophytic mosses are essentially rock plants. Some form close velvety masses on granite and sandstone. Other species occur with *Selaginella rupestris*, and Scytonema, and lichen mats on the dry gravel ridges and on compact limestone débris. Several xerophytic species of liverworts occur upon granite fissures and upon gravelly soils, notably three or four species of Ricciaceae.

HALOPHYTIC VEGETATION.

The areas in the west Texas region in which the soil is impregnated with alkali sufficient to affect the vegetation covering are rather large and widely distributed, and have been but little investigated from a botanical point of view. There are included here in general (1) the gulf coast, (2) basins in the lower Rio Grande plain, (3) the gypsum beds of the red beds country, (4) the alkali basins of the western side of the Staked plains, (5) the Pecos valley or Toyah basin, (6) the bolson basins of trans-Pecos Texas of which the Howard and Hueco bolsons are the largest.

From Dr. Havard's description of the "Pecos flats" and of

Salt lake basin (the Howard basin), it appears that the two types of vegetation on these alkaline flats are grass and chaparral formations. He says (*loc. cit.*, p. 465) "the prevalent grass of the Pecos flats and often the only kind is *Sporobolus airoides*, with erect culm one to three feet high, and loose open panicle. It is distinctly salt to the taste," etc. "On alkaline soils occur the fleshy chenopods *Suaeda suffruticosa* and *S. depressa*, and *Spirostachys occidentalis*." Of the Howard basin he says (p. 497) "the smooth, broad beach of the lakes (occupying the center of this basin) more or less incrusted with alkali is absolutely bare. Here and there low sand hillocks are covered with *Spirostachys occidentalis*, *Larrea Mexicana*, and *Frankenia Jamesii*." The salt grasses of the northern extremity of the basin consist mostly of *Sporobolus airoides* and *S. Wrightii.*

Detailed information of the vegetation of alkaline basins or of the Gulf coast within the region here considered is not sufficient to warrant further discussion.

CHANGES IN PREVALENT FORMATIONS DUE TO AGENCIES OF CIVILIZATION OR OTHER CAUSES.

The equilibrium established upon the vegetation of the west Texas region as a resultant of all the forces playing upon it has been destroyed by the introduction of new forces chiefly due to human agency. As a consequence, the vegetation of the region is undergoing some profound changes. Under the reign of equilibrium the trend was decidedly toward the establishment of solid grass formations, thus making the region one of open grass prairies and plains. The present trend is decidedly toward the establishment of woody vegetation, either shrubby or dwarfed arborescent, with a coincident driving out of sun-loving species (especially grasses) and favoring of the shade-loving ones.

Other changes not in the direction of establishing a woody vegetation are taking place. For example, in the constitution of the grass formations Jared G. Smith observes (Bull. 16, U. S. Div. Agrost., p. 28) "before the ranges were overgrazed, the grasses of the red prairies were largely blue stems or sage

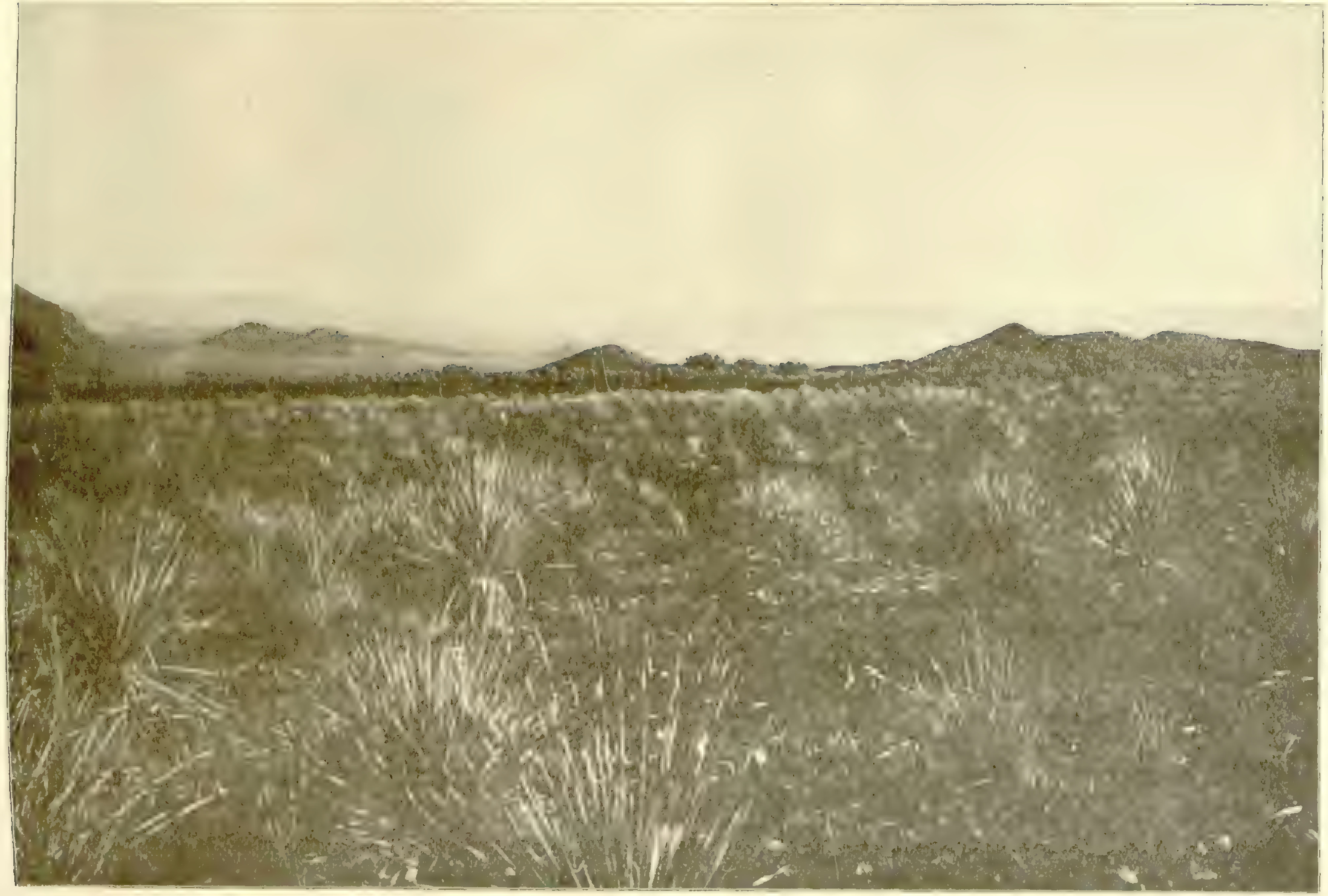

FIG. 24.—Yucca formation on foothills of Chisos mountains, trans-Pecos Texas; Yucca ("palmella") and sotol (*Dasylirion Texanum*); oak in the background probably *Q. Emoryi*.

grasses (Andropogon), often as high as a horse's back. After pasturing and subsequent trampling and hardening of the soil the dog grasses or needle grasses took the whole country. After further overstocking and trampling the needle grasses were driven out and the mesquite grasses (Hilaria and Bulbilis) became the most prominent species."

There is a further strong tendency toward the establishment of a weed vegetation to the disadvantage of what may be called the native vegetation. Such for example are *Gutierrezia Texana* and *Croton Texensis*.

Regarding the establishment of woody vegetation, it is the unanimous testimony of men of long observation that most of the chaparral and mesquite covered country was formerly open grass prairie. This applied to the Rio Grande plain, as well as to the mesquite flats of the central provinces. Illustrations are everywhere at hand. At Austin, for example, many black land pastures have within a few years become covered by a perfect jungle of mesquite.

Apparently under the open prairie régime the equilibrium was maintained by more or less regular recurrence of prairie fires. This, of course, is by no means a new idea, but the strength of it lies in the fact that the grass vegetation was tolerant of fires and the woody vegetation was not. It was only after weakening the grass floor by heavy pasturing and ceasing to ward off the encroaching species by fire that the latter invaded the grass lands. Once the equilibrium was destroyed everything conspired to hasten the encroachment of chaparral—droughts, pasturing, trampling, seed scattering, and so on. As Smith pointed out, a mesquite tree once established became a center of infection in offering shelter for shrubby plants and shade-loving grasses, driving out the native prairie grasses. In brief, the efforts to exploit the wealth of grass lands for profit, namely stock raising, have been the main agency in transforming them rapidly into lands covered by a totally different and far less valuable vegetation.

Another economic question arises from artificial change of plant formations, though exactly the reverse of the preceding discussion, namely, in destroying the woody vegetation of certain areas. The great demand for charcoal, fuel, posts, and rough construction timber, and the desire to secure small patches for temporary cultivation are resulting in a rapid removal of the xerophytic timber vegetation and the cañon timber from the hill country of the Edward's plateau. This brings up the question of the relation of this timber vegetation to the water supply, to soil erosion, and to destructive floods. In some cases, at least, this formation is succeeded by the rock vegetation and the adobe vegetation of the Cretaceous areas, which establish themselves as a result of denudation by erosion which follows removal of the timber covering.

SUMMARY.

1. By reason of its geographic extent and position and of its relief, the west Texas region possesses floral elements ranging in their temperature relation from tropical to transition.

2. In its climatic relations the region falls partly under the eastern or Atlantic type (Gulf type, Great plains type), and partly under the Pacific (Yuma type, Mexican type). This brings about great diversity of vegetation in the moisture relation.

3. This region is the meeting ground of the following floral elements: (1) the Gulf neotropical; (2) the Mexican semitropical; (3) the Austro-riparian and Carolinian; (4) the Great plains upper Sonoran; (5) the north central prairie region; (6) the Rocky mountain; (7) the south plateau (of the Rocky mountains) upper Sonoran; (8) the arid plateau and bolson desert lower Sonoran.

4. The physiographic and geologic provinces coincide in general with vegetation provinces distinguished by characteristic vegetation formations.

5. The flora of the entire region is one of xerophytic aspect, but of several grades from semi-arid to extremely arid. Broad streamways and cañons and high mountains carry mesophytic vegetation into the heart of the region.

6. Annuals whose vegetation period covers only a few weeks exist generally in pure formation in all parts of the region having a constant annual recurrence of temperature and moisture conditions suited to the species in question. Thus the plains from the lower Rio Grande to the Red river and northward may possess successively the same ephemeral but extremely brilliant formations.

7. The vegetation native to the region before the coming of civilization is undergoing profound changes as a result of disturbed equilibrium. This is no doubt exterminating certain species, epecially grasses. The chief results of the changes appear in establishing a woody or weed vegetation, and in the denudation of the hill country.

University of Texas, Austin.

FURTHER NOTES ON THE PHYSIOLOGY OF POLYMORPHISM IN GREEN ALGAE.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXII.

BURTON EDWARD LIVINGSTON.

SINCE the publication of the previous article on this subject[1] several additional lines of experimentation have been completed. The results of these will be given in the present paper. They corroborate the conclusions already expressed, and also throw some further light upon the interesting response with which we are dealing.

I. PHYSIOLOGICAL EXPERIMENTS.

The experiments here recorded were all performed upon the organism used in the previous work, that is, *Stigeoclonium tenue* (?), and the same methods were employed as far as the culture media would allow. The cultures may be classified according to the media used into the following groups: (1) sugar solutions, (2) solutions containing both sugar and mineral salts, (3) porous plate cultures, (4) gelatine cultures, (5) cultures in darkness, (6) evaporation cultures. These categories will be considered in order.

I. SUGAR SOLUTIONS.

The work already published shows clearly that for changes in concentration of Knop's solution the factor controlling the response of the alga is the osmotic pressure. Whether this acts upon the organism merely through a change in the relation of water to the cell, or in some more complex way, could not be decided as long as the pressure was always produced by mineral salts. Thus the next step to be taken was to determine the effect upon the plant of a solution of non-electrolytes. To this end some substance had to be chosen in which the plant would live and grow for some length of time. Also it was necessary that the culture media be of such nature as not to be readily attacked by bacteria and fungi. After several failures, the two saccharoses, lactose and cane sugar, were hit upon for this purpose. The former is far the better, but the latter serves very well. Cultures in these may be continued for two, three, or even four weeks without undergoing fermentation sufficient to affect the alga appreciably.

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[1] LIVINGSTON, B. E.: On the nature of the stimulus which causes the change of form in polymorphic green algae. BOT. GAZ. 30: 289. 1900.

Tables I and II give the results of some representative cultures in these solutions. At the left are those in lactose, at the right those in cane sugar. In the first table the original material was of the palmella form; in the second, of the filamentous. The concentrations are given in terms of a normal solution ($n = 1$ gram molecule per liter), and are placed in the columns headed "concentration." In the columns headed "first response," Sp. F. denotes that zoospores were produced in great numbers, and germinated as usual to form filaments. A single asterisk (Sp.*) shows that the spores did not germinate. Filaments produced from the original masses are denoted by *F* in this column. Two asterisks (Sp.**) show that few zoospores were produced, and that these failed to germinate. *P* denotes the palmelloid form; $P >$ the rounding up of cells as if going over into palmella. In the columns following those indicating the response is given the time of response in days; 2–12 denotes that the response was observed two days after the making of the culture, and continued for ten days. The second response is the result of evaporation, and comes after a somewhat longer time than the first. The time for it is given in days after the making of the culture.

In general, solutions of low osmotic pressure produce zoospores and filaments, while those of high pressure produce only the round-celled form. This is in accord with the results obtained with solutions of mineral salts. However there is one difference in the behavior of the palmella form in solutions of electrolytes and non-electrolytes. This is brought out by Table

TABLE I.

PALMELLA IN SUGAR SOLUTIONS.

LACTOSE					CANE SUGAR				
Concentration	1st Response	Time	2d Response	Time	Concentration	1st Response	Time	2d Response	Time
$\frac{n}{100}$	Sp. F.	2–12	P	30	$\frac{n}{100}$	Sp. F.	5–10	..	..
$\frac{n}{100}$	Sp. F.	2–7	..	..	$\frac{n}{100}$	Sp. F.	2–9	..	..
$\frac{n}{10}$	Sp. F.	4–9	P	30	$\frac{n}{10}$	Sp. F.	3	..	..
$\frac{n}{10}$	Sp. F.	9	..	..	$\frac{n}{10}$	Sp. F.	2–18	..	..
$\frac{2n}{10}$	Sp. F.	2–12	..	..	$\frac{2n}{10}$	Sp. F.	2–18	..	..
$\frac{3n}{10}$	Sp.* F.	2–7	P	9	$\frac{3n}{10}$	Sp. F.	2–18	P	30
$\frac{4n}{10}$	Sp.** F.	2	P	14	$\frac{4n}{10}$	Sp. F.	8–14	..	..
$\frac{5n}{10}$	No spores P	14	..	..	$\frac{5n}{10}$	Sp.* F.	8	P	14
$\frac{7n}{10}$	P	10	..	..	$\frac{7n}{10}$	P	10	..	..

TABLE II.

FILAMENTS IN SUGAR SOLUTIONS.

LACTOSE			CANE SUGAR		
Concentration	Response	Time	Concentration	Response	Time
..	..	..	$\frac{n}{100}$	Sp. F.	6–13
..	..	..	$\frac{n}{10}$	No spores F	6
..	..	..	$\frac{n}{10}$	Sp.* F P>	4–11
$\frac{3n}{10}$	No spores P>	10	$\frac{3n}{10}$	No spores P>	14
$\frac{5n}{10}$	P	14	$\frac{5n}{10}$	P	8–14
$\frac{5n}{10}$	P	10	$\frac{5n}{10}$	P	10–12
$\frac{7n}{10}$	P	10	$\frac{7n}{10}$	P	10
..	..	..	$\frac{75n}{100}$	P	9

III, which shows the maximum limit for zoospore production in each case. It is to be compared with Table V of the former article,[2] from which the figures for mineral solutions have been taken. The figures have been altered to round numbers to avoid confusion.

TABLE III.

MAXIMUM LIMITS FOR ZOOSPORE PRODUCTION.

Original Form	Mineral Solutions	Solutions of Non-electrolytes	
		Lactose	Cane Sugar
Palmella	$\frac{2n}{10}$	$\frac{5n}{10}$	$\frac{6n}{10} - \frac{7n}{10}$
Filamentous	$\frac{3n}{10}$	$\frac{3n}{10}$	$\frac{3n}{10}$

The filamentous form responds in exactly the same manner whether the solution is of electrolyte or non-electrolyte. But to bring about an inhibition of zoospore production in the palmella form requires a much higher osmotic pressure when this is produced by non-electrolytes than in the other case. Also the two sugars used differ in that the limit for cane sugar is much higher than for lactose. Why is this? The volume of the cells in the culture is so small, as compared with that of the surrounding fluid, that the difference just spoken of cannot be explained by the supposition that the carbohydrate is absorbed and thus the concentration of the medium lowered. The amount of absorption possible would be entirely inadequate to alter the concentration to any appreciable degree. It seems more probable that by absorption of sugar the concentration of the cell sap is increased, thus decreasing the difference between the osmotic conditions within and without the plant, and so weakening the stimulus. This would occur if the carbohydrate molecules were to penetrate the cells (*i. e.*, be absorbed) more rapidly than the ions of an electrolyte. It is possible that cane sugar is absorbed much more readily than lactose; hence might arise the difference between the effect of these two substances upon the organism.

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[2] *Loc cit.*, p. 313.

Considering these results, together with those heretofore published, there seems little room for doubt that the response of this plant is brought about by a change in its relation to water. An increase in the osmotic pressure of the surrounding fluid must invariably extract water from the cell (since plant membranes are readily permeable to water), and a decrease of such pressure must cause the cell to take up more. However, an increase in the amount of sugar in the medium might influence the plant otherwise than in the way just mentioned. There might be, for instance, a chemical effect produced by the carbohydrate molecules. Also, it is readily conceivable that an increase in the number of electrically charged ions in the medium might exert some specific influence upon the protoplasm aside from mere change of water relation. But it is hardly conceivable that any chemical influence exerted by sugar molecules could be identical in its effect with an influence exerted by electrolyte ions. Thus we are almost driven to the following conclusions: (1) since solutions of electrolytes and non-electrolytes affect the organism in the same way, they must exert a common influence upon the cells; and (2) since it is inconceivable that there is any chemical influence common to the two forms of solution, the response must be due to the *one factor which is common to both*, namely, change in the water relation. Whether this change in the water content of the cells acts merely through the mechanical effects of a change in the turgor pressure of the cell sap, or whether the response is brought about by a more subtle adjustment within the protoplasm itself, we have at present no means of telling. It seems probable that both these factors are operative.

It is of interest to note here that while the organism often dies in a mineral solution whose pressure is $\frac{4n}{10}$, and invariably dies in stronger mineral solutions, yet it lives indefinitely and apparently without injury in a normal sugar solution. This is probably due to the poisonous action of some of the electrolyte ions used. To determine, if possible, what this action may be, will be the object of further research.

The same culture may be made to change its form several times in sugar solutions just as in mineral solutions, by adding water or allowing it to evaporate. Nearly all the cultures made in sugar solutions have been controlled by others made at the same time in mineral solutions, and the control cultures have not deviated at all from those discussed in my previous paper. Further, healthy material taken from sugar solutions behaves in water and in mineral solutions precisely as though it had been grown in a mineral solution.

2. MIXED SOLUTIONS.

These solutions contained both sugar and mineral salts. The response of the alga to the weaker ones is the same as though they were composed either of sugar alone or of salts alone. For the stronger solutions the same is true of the filamentous form. But the palmella form gives something of its characteristic response to sugar or electrolytes, according as one or the other of these substances predominates. However, this was not very well marked in the experiments. In general, the plant behaves in the same manner in a mixed solution as in a simple one.

2. POROUS PLATE CULTURES.

These were made on unglazed porcelain, such as is used in chemical work. A piece of plate four or five centimeters square was laid on the bottom of the culture dish, and sufficient solution was poured over to stand within a millimeter or two of the upper surface of the plate. Thus the plate was saturated, but no free liquid was upon its surface. The alga cells were placed upon the plate and the whole was covered as usual. The results of these cultures are perfectly uniform, and are exactly what would have been expected. The osmotic pressure of the solution which saturates the plate determines the response of the plant. Typical results from the series of plate cultures are presented in table IV. The abbreviations are those used in tables

I and II. Ev denotes an uncovered culture with rapid evaporation.

TABLE IV.

POROUS PLATE CULTURES.

Solution.	Original form.	Response.	Time.	Solution.	Original form.	Response.	Time.
$\frac{n}{100}$ L	P	Sp. F.	9	$\frac{3n}{10}$ K	P	P.	10
$\frac{n}{100}$ S	P	Sp. F.	9	$\frac{4n}{10}$ S	P	Sp. F.	9
$\frac{n}{100}$ K	F	Sp. F.	10	$\frac{4n}{10}$ K	P	P. F.	16
$\frac{n}{10}$ K	F	P. F.	10	$\frac{5n}{10}$ L	P	P.	16
$\frac{2n}{10}$ L	P	Sp. F.	9	$\frac{75n}{100}$ L	P	P.	46
$\frac{3n}{10}$ K	F	P. F.	10	$\frac{n}{100}$ L, Ev	F	P.	6

4. GELATINE CULTURES.

These were made like the plate cultures just described, excepting that in the place of the porcelain support the solution to be used was thickened with gelatin until it would give a firm surface on which to place the alga. The result was uniform with the foregoing. The gelatin itself has no influence. The osmotic pressure of the solution determines the response of the organism. Gelatin cultures cannot be continued very long because of bacterial action, and are therefore not very satisfactory.

5. CULTURES IN DARKNESS.

In darkness the alga remains green and healthy for three to five weeks. At last the cells become plasmolyzed and go to pieces. Putting the culture in darkness has no effect whatever upon the response of the plant. This probably indicates that the mechanism of polymorphism is not connected with that of photosynthesis.

6. EVAPORATION CULTURES.

Weak solutions, with their contained filaments, may be left open to the air, and within a few days become very much concentrated through evaporation. The response of the plant is rapid and marked in these cases. If one has filaments and wishes the palmelloid form, he has but to leave the dish uncovered for a few days to attain this end. Evaporation affects the plant in the same way whether it be in the case of sugar solution, mineral solution, or porous plate culture. It was impracticable to get results by evaporation from gelatin on account of bacteria, by the growth of which the culture was destroyed before a response could be expected.

SUMMARY.

1. Non-electrolyte solutions have the same effect as electrolyte solutions; the osmotic pressure is the controlling factor in determining the form of the plant. This is effective through changes in the water content of the cells.

2. The threshold of stimulation for inhibition of zoospore production is at a higher concentration in a solution of non-electrolytes than in one of electrolytes. Also, the plant withstands the killing effect of the solution at a higher concentration for non-electrolytes than for electrolytes.

3. This threshold of stimulation for the palmella form is at a higher concentration for cane sugar than for lactose.

4. Cells supported upon gelatin or porcelain plates moistened by a solution respond in the same way as though they were immersed in the solution.

5. Prolonged darkness has no effect upon the form of the plant; the response of polymorphism does not depend upon the photosynthetic process.

6. Increase in concentration caused by evaporation from any solution or from porcelain plates brings about the normal response for a concentrated solution.

II. PHYSICO-CHEMICAL TESTS.

In order to determine the extent of the error introduced into these experiments by the author's assumption[3] of complete ionization in the mineral solutions, a series of tests of the actual osmotic pressures developed therein has been carried out during the past summer.

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[3] *Loc. cit.*, p. 297.

Owing to the as yet insurmountable difficulties in determining directly the osmotic pressure of a solution, the indirect method by freezing points was resorted to. It has been well established[4] that for dilute solutions a uniform relation obtains between the osmotic pressure, the depression of the freezing point, and the elevation of the boiling point. Thus if Δ_f denotes the depression of the freezing point, the osmotic pressure is given by the formula $P_f = 12.07\,\Delta_f$, wherein P_f is the osmotic pressure at the freezing point of the solution. Similarly, $P_b = 57\,\Delta_b$, wherein P_b is the osmotic pressure at the boiling point and Δ_b the elevation of the boiling point. The depression of the freezing point was determined by means of Beckmann's apparatus,[5] for the mineral solutions described in the previous paper, as far as these were at hand when the tests were made. From these data the osmotic pressure at the freezing point (practically 0° C.) was derived by the formula given above, and from this the pressure at 25° C. was obtained by the formula $P_t = P_f\,(1 + 0.00367\,t)$,[6] wherein P_t is the pressure at any given temperature (t).

Since ionization is usually more complete at high temperatures than at low ones, it was thought advisable to make some sample tests of osmotic pressure by determining the elevation of the boiling point. This was done for a limited number of solutions only. For this purpose the improved apparatus of Beckmann[7] was used. After the determination of P_f and P_b (*supra*), P_{25} was obtained by interpolation between them thus: $P_{25} = P_f + 25 \times 0.00367\,(P_b - P_f)$. The results show that the difference between the degree of dissociation at 0° C. and at 25° C. is so small as to be neglible for our present purpose.

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[4] NERNST, W.: Theoretical chemistry, translated by C. S. Palmer, p. 123 *et seq.* 1895.

[5] BECKMANN: Zeitschr. Physik. Chem. **2**: 638. 1888.

[6] Simply the law of Gay-Lussac, which holds for osmotic pressures of weak solutions. NERNST: *op. cit.*, p. 134 *et seq.* Also OSTWALD, W., Outlines of general chemistry, translated by J. Walker, p. 128 *et seq.* 1895.

[7] BECKMANN: Zeitschr. physik. Chem. **8**: 223. 1891.

The data obtained by these tests of the actual molecular conditions within these solutions are given in Table V. This is a supplement to the table given in the author's previous paper on this subject. In the first column are given the so-called percentage strengths of the solutions employed. In the second the solutions are designated by the letters previously used for that purpose (*loc. cit.*, p. 599). The next two columns contain the depressions of the freezing point and the elevations of the boiling point as directly observed. Then follow the two columns containing the osmotic pressures at the freezing and boiling points given in atmospheres. These numbers were obtained from Δ_f and Δ_b by the formulae given above. In the next two columns are given the pressures at 25° C., measured in centimeters of mercury, 1 being found from P_f by direct application of the law of Gay-Lussac, 2 by interpolation between P_f and P_b. The last column contains the pressures originally calculated by the assumption of complete ionization. They are introduced here for comparison.

It will be noted that there is a considerable range in the actual osmotic pressures of the different solutions whose calculated pressures are the same. This would be expected and is partially due to variations in the degree of ionization of the different salts according to their influence upon one another. It is also in part brought about by the fact that K_2HPO_4 dissociates completely only in very weak solutions. But this range of pressures lies entirely within the range of the pressure limits found for the several responses of the plant (*loc. cit.*, pp. 301, 306, 313). That is, the errors of calculation, while very large from a physical point of view, are not large enough to affect the physiological conclusions already expressed. This is on account of the comparatively low degree of sensitiveness of the organism with which we are dealing.

Discussion of the reasons for the curious variations from the calculated pressure manifested by these tests will be reserved

TABLE V.

PRESSURE DATA FOR NUTRIENT FLUIDS.

Per cent.	Solution	Δf	Δb	P_f (Atm.)	P_b (Atm.)	P_{25} (cm. Hg) (1)	P_{25} (cm. Hg) (2)	P (Calc.) (cm. Hg.)[8]
0.005	A	.023	....	.2776	....	23.0288	....	16.19
	C	.012	.005	.1448	.285	12.0148	13.6701	
	D	.032	....	.3862	....	32.0475	....	
0.1	A	.032	....	.3862	....	32.0475	....	32.37
	C	.058	....	.7001	....	57.9861	....	
	D	.041	....	.4949	....	41.0605	....	
0.5	K	.154	.061	1.9088	3.477	158.3460	172.9608	161.86
	A	.124	....	1.5967	....	132.4809	....	
	B	.155	....	1.8708	....	155.2300	....	
	C	.165	....	1.9915	....	165.2392	....	
	D	.185	....	2.2329	....	185.2728	....	
1.0	K	.3	....	3.621	....	299.896	....	323.71
	A	.235	.06	2.8364	3.42	235.3416	228.5578	
	B	.26	....	3.1382	....	260.3836	....	
	C	.295	....	3.5606	....	295.4348	....	
	D	.322	....	3.8865	....	322.4756	....	
1.5	K	.4	.09	4.828	5.13	400.368	369.0180	487.59
	A	.32	....	3.8634	....	320.5604	....	
	B	.381	....	4.5987	....	374.1936	....	
	C	.433	....	5.2263	....	433.6408	....	
	D	.465	.12	5.6125	6.84	465.7100	449.8644	
2.0	A	.415	.1	5.0007	5.7	414.9296	393.3380	647.42
	B	.46	....	5.543	....	459.9216	....	
	C	.56	....	6.8444	....	567.9024	....	
	D	.682	.15	8.2317	8.55	683.009	631.6588	

for a future paper. These data are published here merely as corroboration of the general conclusions already published. I wish to express my thanks here to Dr. Felix Lengfeld, of the Kent Chemical Laboratory of this University, for much kind advice and for the unrestricted use of the necessary facilities for such determinations as the above.

HULL BOTANICAL LABORATORY,
THE UNIVERSITY OF CHICAGO.

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[8] See the author's previous paper, *loc. cit.*, pp. 301, 306.

BRIEFER ARTICLES.

INTRAMOLECULAR RESPIRATION.

THE experiment which is reported here failed in its original purpose, but the results which it did furnish seem to be worth reporting. The experiment was run in duplicate. Five grains of Japanese buckwheat, which had been previously soaked in distilled water for six hours, were placed in each of two eudiometers of 114^{cc} capacity. A piece of moist absorbent cotton was then placed loosely on the seeds, and the whole was secured in place by a cork with a groove in one side to admit of free circulation of the gases above and below. The volume of the seeds, cotton, and cork in the first eudiometer was 14.5^{cc}, and in the second 15.5^{cc}. The eudiometers were partly filled with mercury and inverted over a dish of the same metal. The column of mercury in no. 1 was 137^{mm}, and in no. 2 132^{mm} high. After reducing to standard pressure, no. 1 contained 65.41^{cc} and no. 2 contained 65.11^{cc} of atmospheric air.

The evolution of carbonic acid gas was quite rapid for the first few days. In forty-eight hours the volume of gases had increased so much that the column of mercury was entirely displaced and the gases had begun to escape through the dishes of mercury. This loss of gas seemed to invalidate the experiment, consequently the apparatus was set to one side until they could be again fitted up.

Some four weeks later it was decided to repeat the experiment with a smaller quantity of seeds; but before doing so 2^{cc} of strong caustic potash solution was introduced into each of the eudiometers to absorb any carbonic acid gas that might be present. An hour and ten minutes later it was found that the column of mercury in no. 1 had risen 215^{mm}, and in no. 2, 220^{mm} above the level of the dish, the temperature being 21° C. as at the beginning of the experiment. Thus, there was remaining in no. 1, after reducing to standard pressure, 32.49^{cc}, and in no. 2, 26.92^{cc} of gases. No. 1 contained, when the caustic potash solution was introduced, 99.5^{cc}, and no. 2, 98.5^{cc} of gases; hence no. 1 must have contained 67.01^{cc} of carbonic acid gas, of which, on the assumption that atmospheric air is 21 parts oxygen and 79 parts nitrogen, 53.28^{cc} was evolved by intramolecular respiration, and no. 2, 71.58^{cc}, of which 57.91^{cc} came from the same source.

If 0.21 of the atmospheric air in the eudiometer at the beginning of the experiment was oxygen, and 0.79 nitrogen, then no. 1 must have contained 51.67^{cc} and no. 2 51.44^{cc} of nitrogen. Now at the close of the experiment, assuming that no other gas was present, no. 1 contained 32.49^{cc} and no. 2, 26.92^{cc} nitrogen; therefore 19.18^{cc} of nitrogen must have escaped from no. 1, and 24.52^{cc} from no. 2. On the assumption that the gases were completely diffused, the nitrogen that escaped from the first eudiometer must have carried with it 26.65^{cc}, and that from the second 38.62^{cc} of carbonic acid gas. This shows that from the seeds in the first eudiometer 79.93^{cc}, and in the second 96.53^{cc} of carbonic acid gas must have been evolved by intramolecular respiration.

To explain this apparent discrepancy between the two results, it should be stated that germination had not proceeded so far in no. 1 as in no. 2; in the former the sprouts on the seeds were from 2 to 4^{mm}, and in the latter from 4 to 6^{mm} in length. Slight decomposition had taken place in both eudiometers, but no fungus was visible in either.—T. C. JOHNSON, *West Virginia University.*

NOTES ON AQUILEGIA CANADENSIS LINN. AND A. VULGARIS LINN.

FOR several years I have had growing in my dooryard a patch each of our common eastern columbine and of the European or garden species, and have found them a fruitful source of pleasure and study. I wish to record a few of the more interesting observations. When the buds develop in the axils of the leaves, they at first stand erect, but soon begin to droop, and by the time the flowers begin to expand they hang completely inverted. As soon as the pollen has been shed and the ovaries have been fertilized, the flowers begin gradually to resume the erect position, and by the time the outer whorls have fallen the five-parted ovaries are standing erect, ready to mature, dehisce, and scatter the seeds. This rapid change in the position of the flowers is made possible by the great and rapid changes in the length and thickness of the peduncles. At first they are about one-fourth inch long and very slender; by the time the flowers have fallen and the ovaries are standing erect the peduncles have grown to be three to five inches long, and are thick rigid stems. This entire change takes place in about five days.

As soon as the petals separate at the apex, the five styles protrude and are ready to receive the pollen from other flowers, and before the anthers in the same flower are ready to shed pollen. The numerous stamens stand straight, around the pistil, except while the flowers first open and while the pistil is receiving pollen. At this time the outer ends of the filaments are bent outwards and away from the pistil at an angle of about 45°. As the innate anthers mature, however, and are ready to shed pollen, the filaments gradually assume the erect position. The pistils of the same flower by this time have had ample opportunity to receive pollen from other flowers. The stamens are from one-eighth to one-half inch shorter than the mature pistils. Hence close pollination is avoided by the protogynous condition of the flower, and by the stamens being shorter than and turned away from the stigmas.

The form and disposition of the spurs is quite different in the two species. In *A. Canadensis* the spurs are straight, while in *A. vulgaris* the outer end is curved inwards until it is again bent back on itself, forming an entire ring or circle. In *A. Canadensis* the spurs are longer and more slender and the tissues more tender. In both the nectary is located in the outer end of the spur, where it is represented by a hard nodule or gland. The common ruby-throated humming bird (*Trochilus colubris* L.), the tobacco and tomato sphinx moths (*Macrosila carolina* L. and *M. 5-maculata* Harr.) are common visitors to *A. Canadensis*, but I have never seen them visit *A. vulgaris*.[1] They take nectar by inserting the bill or tongue into the hollow of the spur, while the flower is still hanging in the inverted position. The body of the bird or insect is poised in the air by the rapid motion of the wings. This disturbs the air in the neighborhood violently, and so scatters the pollen widely in all directions.[2] In both species the Virginia carpenter-bee (*Xyocopa Virginica* L.) and a small bee (*Odynerus foraminatus* Sauss.) slit the tube of the spur, and take the nectar direct from the gland. Later, the honey bee (*Apis mellifica* L.) and a green bee (*Agapostemon radiatus* Say) enter these slits and secure the remaining nectar, but they do not make new slits themselves.—J. SCHNECK, *Mt. Carmel, Ill.*

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[1] Perhaps for the reason that the curvature of the spurs of *A. vulgaris* renders it impossible for them to reach the nectar by the usual route.

[2] The inverted position of the flowers at this time renders it impossible for the pollen to fall into the open mouths of the spurs, and so be lost and useless to the flowers for pollination.

CURRENT LITERATRUE.

BOOK REVIEWS.

Guide to garden plants.[1]

THE intention of the writer has been to produce a book which will be of use to amateurs and also to those engaged professionally in horticulture. It deals with the description, cultivation, and propagation of the better known flowers, fruits, and vegetables suitable for growing in the British Islands. The subjects discussed are of such a comprehensive nature that it is quite impossible to expect that even a few of them should be treated in an exhaustive way within the limits of a single volume. A commendable feature — absent in other books on this subject — is a chapter devoted to the life history of plants, which is given in such a manner as to be readily understood by those not versed in technical language. The chapter on the description, cultivation, and propagation of the hardy fruits best suited to the climate of Great Britain gives little help to those in quest of such information in this country. Nearly a thousand pages are devoted to the description of the common plants in cultivation. The plants are arranged in their natural orders, cultural details are given in the majority of cases, and in this part of the work there is a similarity to what is found in the dictionaries of Paxton, Johnson, Nicholson, and Bailey. There is, of course, much in the book which will interest American readers; but, having been written for garden lovers in another part of the world, it would be a dangerous one to put in the hands of the uninitiated in this country, where not only the cultural details differ, but the species and varieties recommended as best would, in very many instances, be entirely unsuited to the conditions existing here.— G. W. OLIVER.

NOTES FOR STUDENTS.

ROSTOWZEW recommends two methods for drying plants which blacken readily.[2] One consists in using between the plants single layers of absorbent cotton 2^{cm} thick, covered with tough tissue paper, in a wire press, placed in a warm place. The other uses a perforate metal cylinder, to be covered with plants between sheets of filter paper held in place by a muslin jacket. The cylinder is covered with a lid and placed over a lamp. The plants dry in an hour or so.— C. R. B.

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[1] WEATHERS, JOHN: A practical guide to garden plants and best kinds of fruits and vegetables. Large 8vo. pp. xii+1192. *figs. 163.* New York City: Longmans, Green, & Co., 1901.

[2] Flora **88**: 473–478. 1901.

NEWS.

JOSEPH Y. BERGEN, the author of well-known text-books on botany, has resigned his position in the English High School of Boston. With his family, he sailed on September 3 for Naples, Italy, where for the future he will make his home.—*Science.*

DR. EDWIN MEAD WILCOX has resigned his position at the Oklahoma Agricultural College and Experiment Station to accept the chair of biology in the Alabama Polytechnic Institute at Auburn. He entered upon his new duties the first of October.

MR. J. B. DANDENO, assistant in the Botanical Museum and in botany at Harvard University, has been appointed a teacher of botany in the St. Louis Normal and High School. DR. N. L. T. NELSON, formerly a fellow of the University of Chicago, has also been appointed to a similar position in the same institution.

DR. J. N. ROSE returned from his third Mexican journey about September 10, having been absent ten weeks. He has brought back a collection containing more than 1,100 numbers, made chiefly in the states of Mexico, Hidalgo, Vera Cruz, and Pueblo, although work was also done in Jalisco and Morelos. Considerable collecting was done in the high mountains, especially about Pachucha and on Orizaba and Popocatepetl. Two trips were made to the latter mountain, and a very full set of its plants obtained, with careful aneroid records of all the higher species. The collection is especially rich in Oxalis, a genus which reaches a high development in Mexico.

A VERY SUCCESSFUL GATHERING of botanists was held in Geneva, Switzerland, on August 6, 7, and 8, when a program, that had been previously distributed, was closely carried out. About sixty members were in attendance, a surprisingly large number considering that no papers were read, and only a single topic was brought forward for discussion beside the details of organization.

Informal business and social matters occupied the first day. On the second day the congress formally opened in the botanical rooms of the University of Geneva, with Dr. Casimir de Candolle as honorary president, Professor R. Chodat as active president, and Dr. J. P. Lotsy as secretary. As announced in the preliminary circular, the question of establishing an international botanical journal, in which reviews of publications shall clearly indicate the merit of the work set forth, was taken up and warmly discussed in all its phases. It was decided to found such a journal, contingent upon securing a sufficient number of subscriptions to maintain it. Dr. Uhlworm was chosen editor for a period of five years, and the new journal is to replace the *Botanisches Centralblatt*, which in consequence will be discontinued after the close of the present year.

During the afternoon the botanical gardens of the university and the famous DeCandolle herbarium were visited, and in the evening a brilliant reception was held, tendered to the congress by the city of Geneva. The last day of the meeting was given up to visits to the Barbey-Boissier herbarium at Chambésy and the gardens of M. Micheli at Jussy, with an elaborate banquet in the evening at the Eynard palace, tendered by the canton of Geneva. At this dinner the menu and the toasts had a strong international coloring, within European limits. After adjournment an excursion through the valley of the Saas to observe alpine plants was conducted by Professor Chodat.

The Americans in attendance at the congress were Mr. David G. Fairchild, of the United States Department of Agriculture; Mr. F. E. Lloyd, of Columbia University; Dr. D. S. Johnson, of Johns Hopkins University; Dr. H. von Schrenk, of the Missouri Botanical Gardens; Mr. and Mrs. W. Murrill, of Cornell University; and Dr. and Mrs. J. C. Arthur, of Purdue University. The meeting was fortunate in having pleasant weather; the local management was untiring in forwarding the interests of the meeting and in providing for the comfort and enjoyment of the members, and the opinion was unanimous that the gathering had been unusually enjoyable and successful. The next meeting of the Société Internationale de Botanique will be held in 1904 in Vienna, under the presidency of Professor Goebel, of Munich, Professor F. O. Bower, of Glasgow, being vice-president, and Dr. J. P. Lotsy, of Tjēbodas, Java, secretary.—J. C. ARTHUR.

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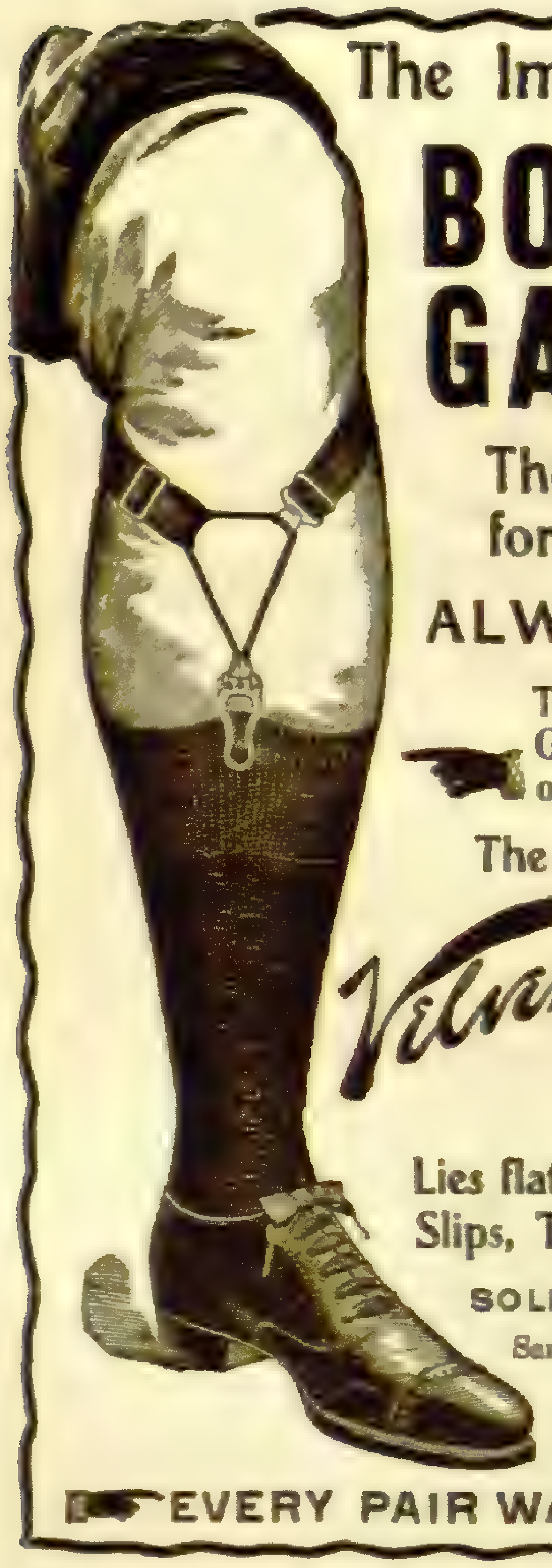

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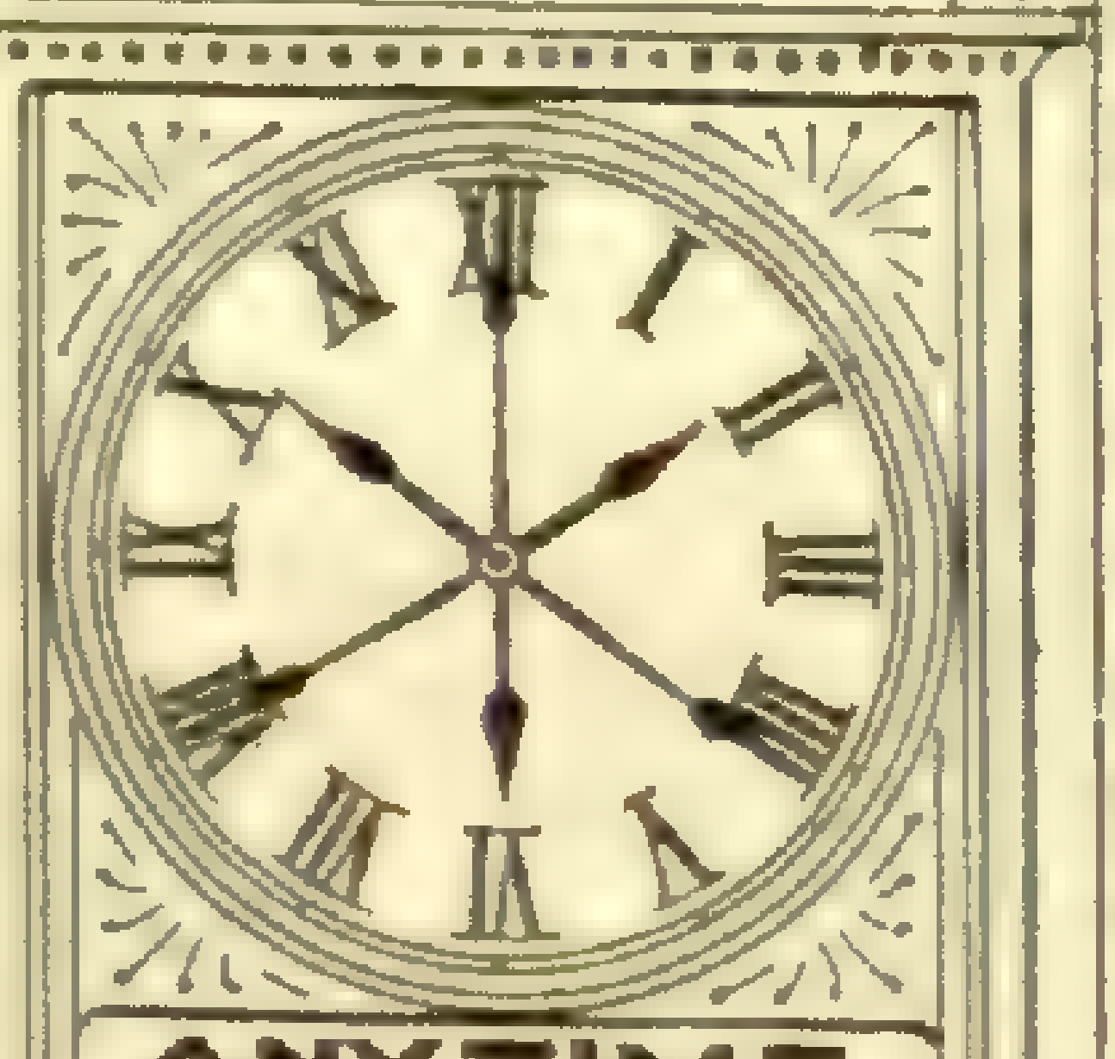

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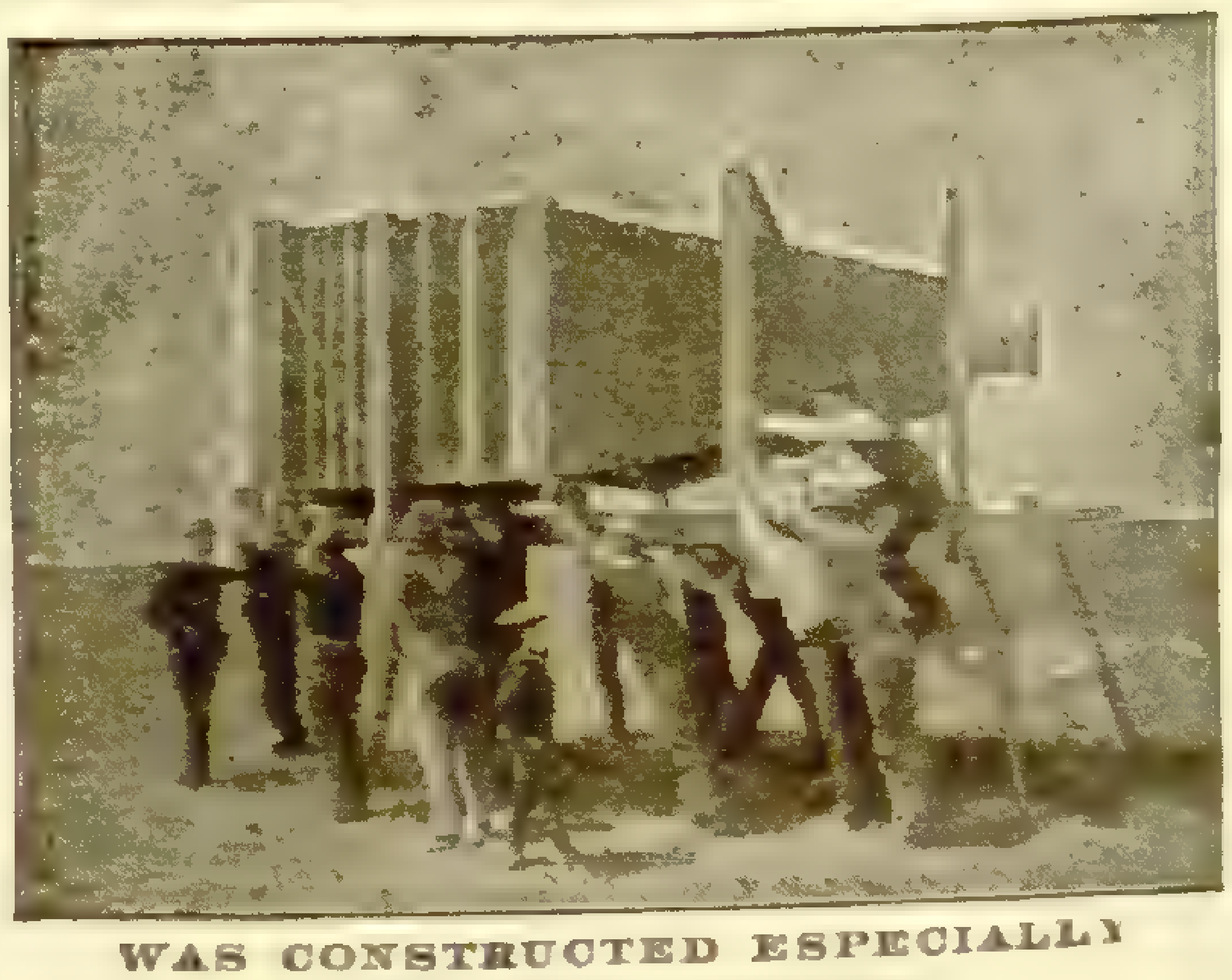

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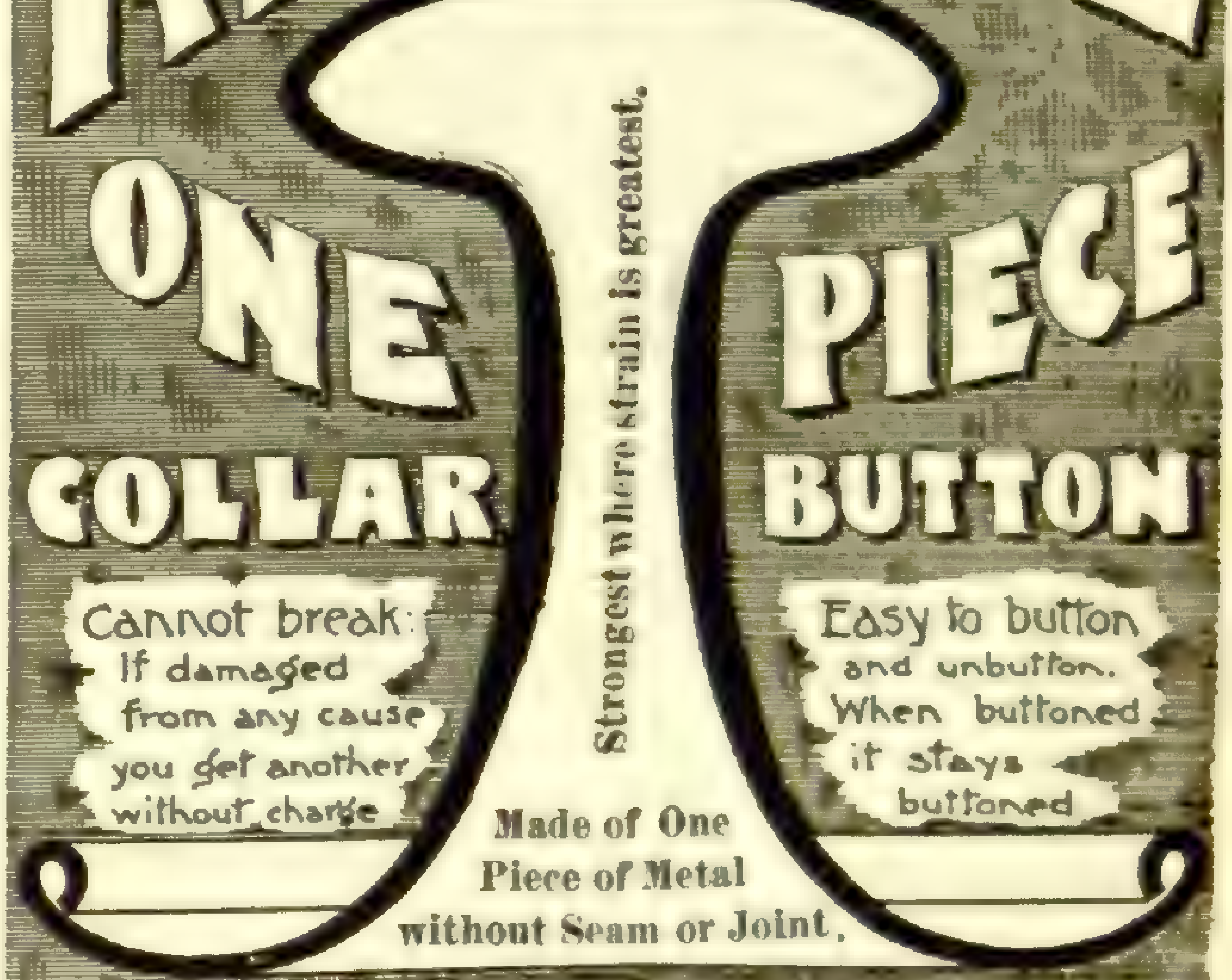
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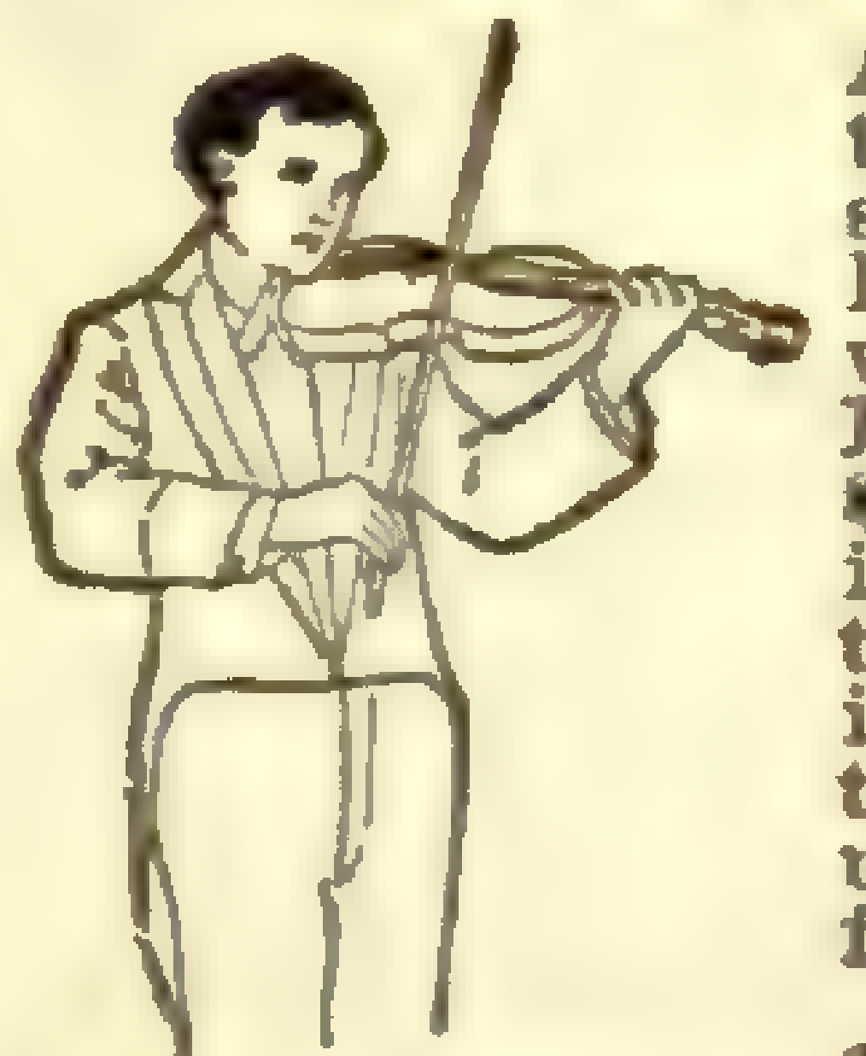

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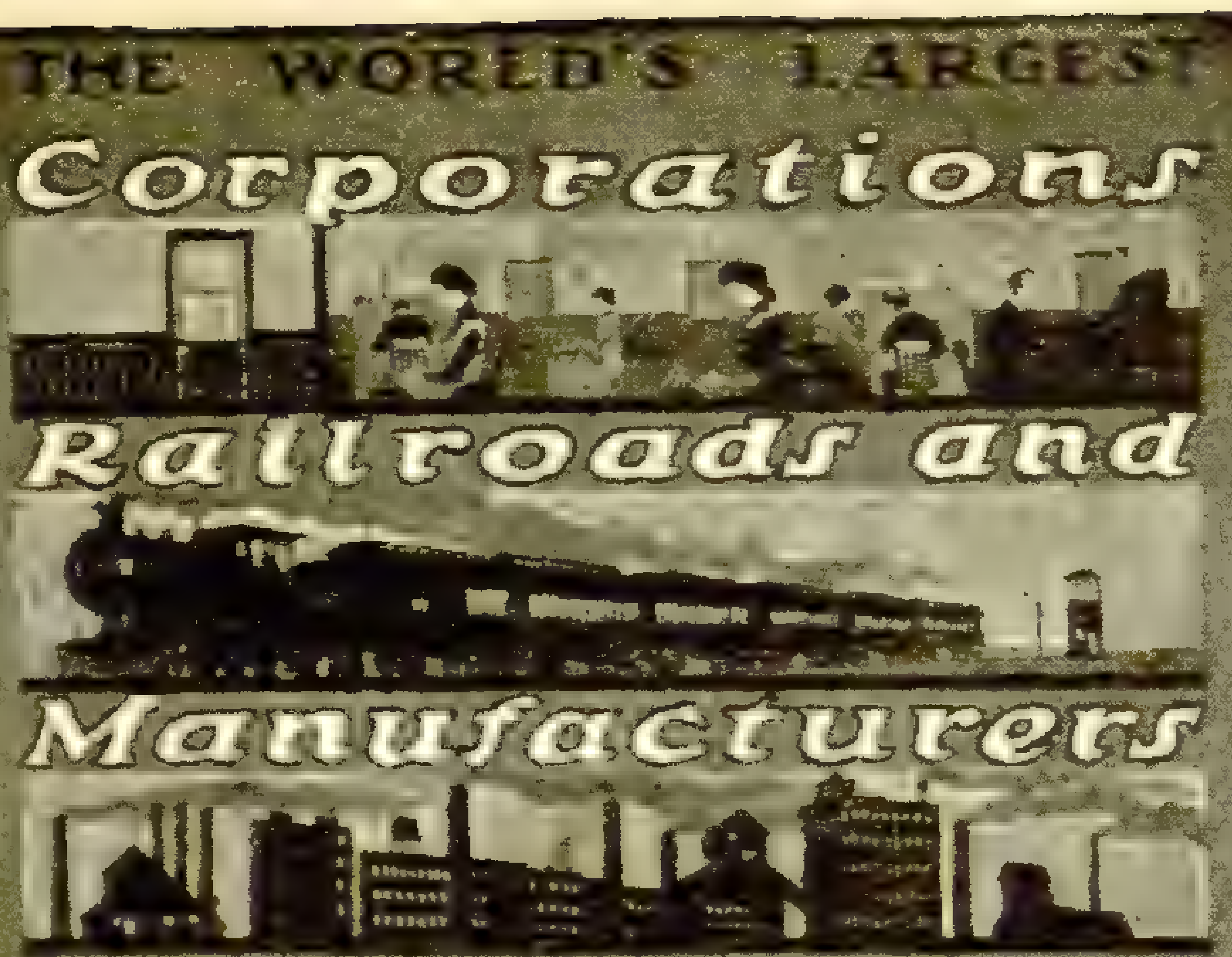

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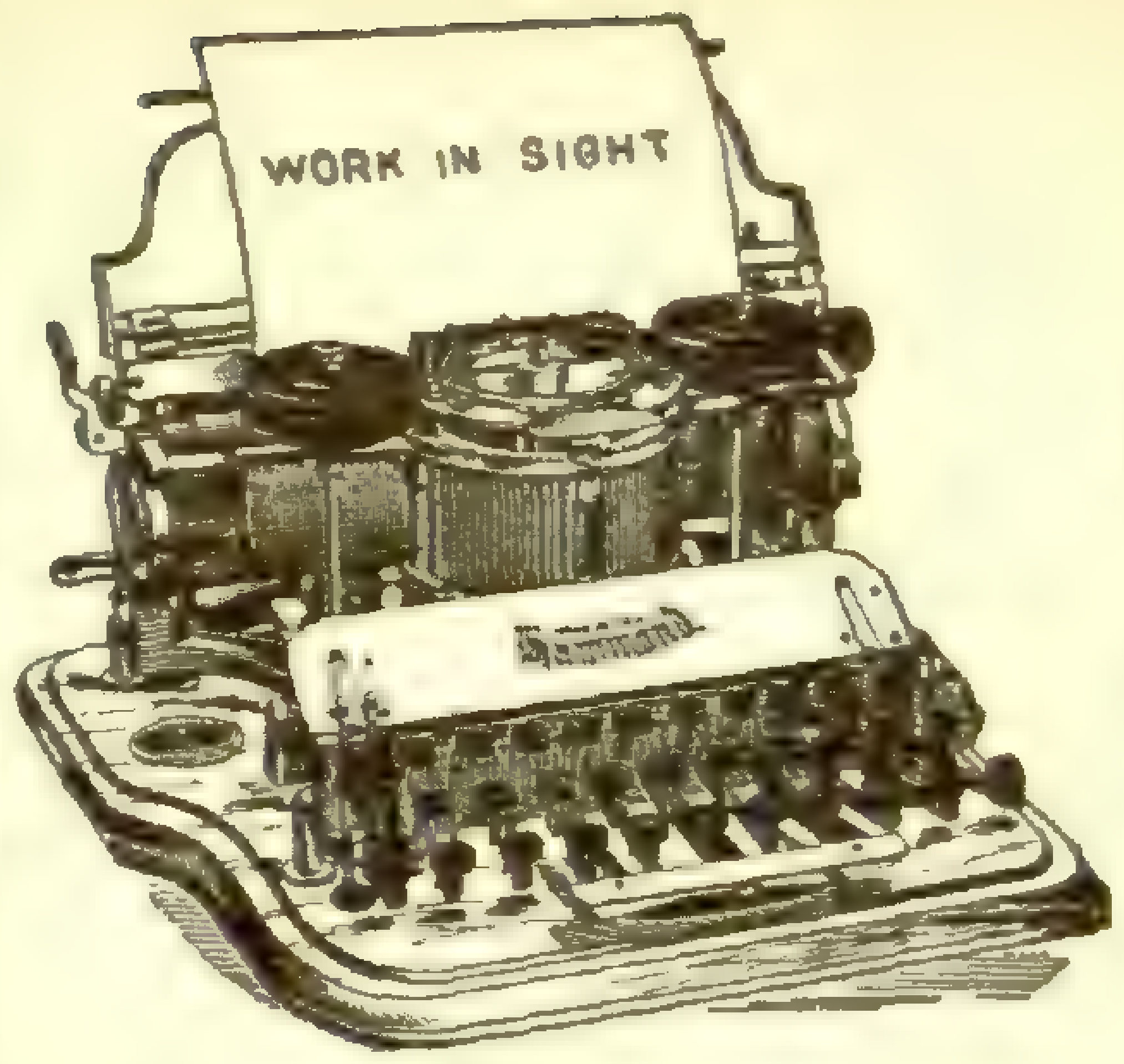

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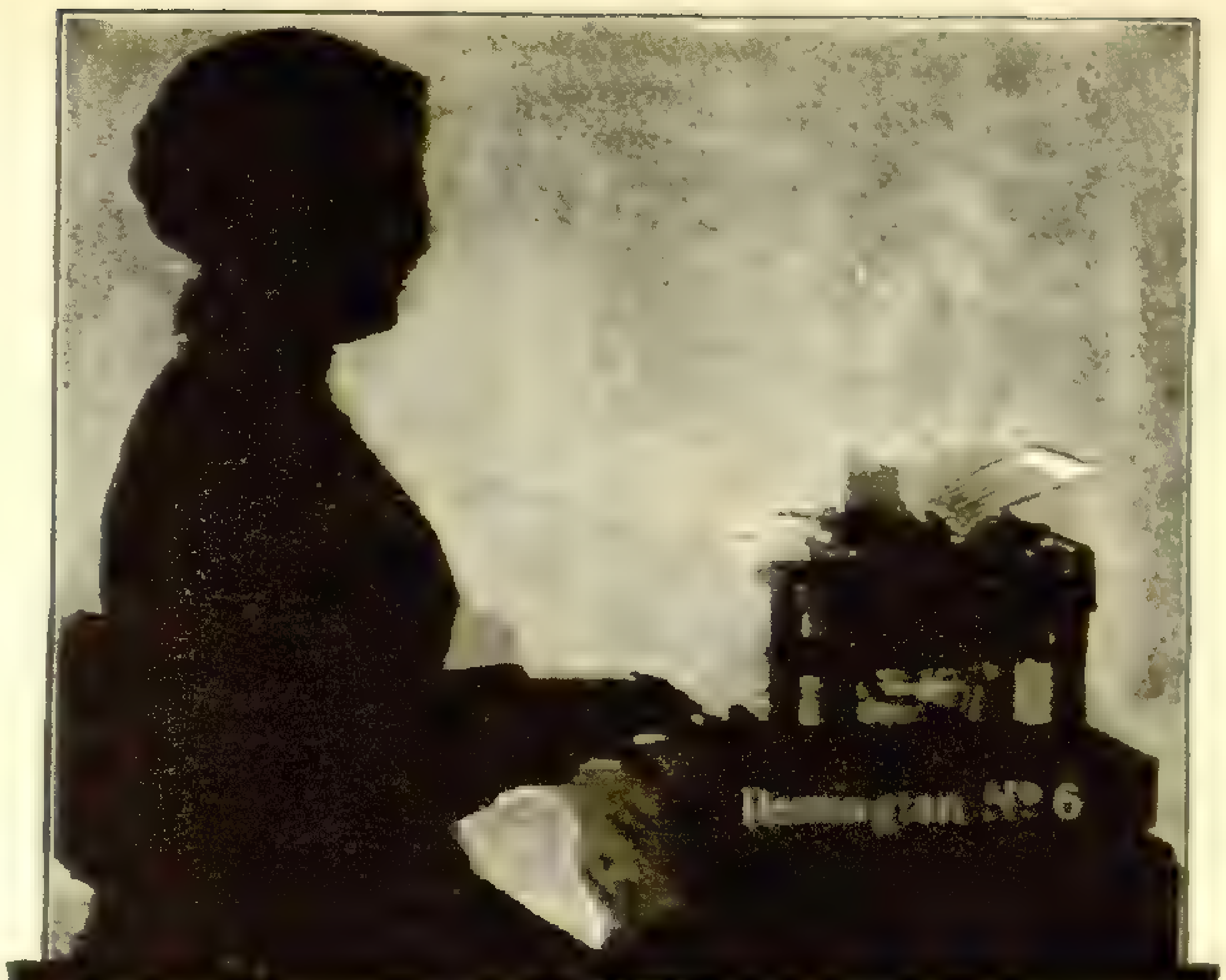

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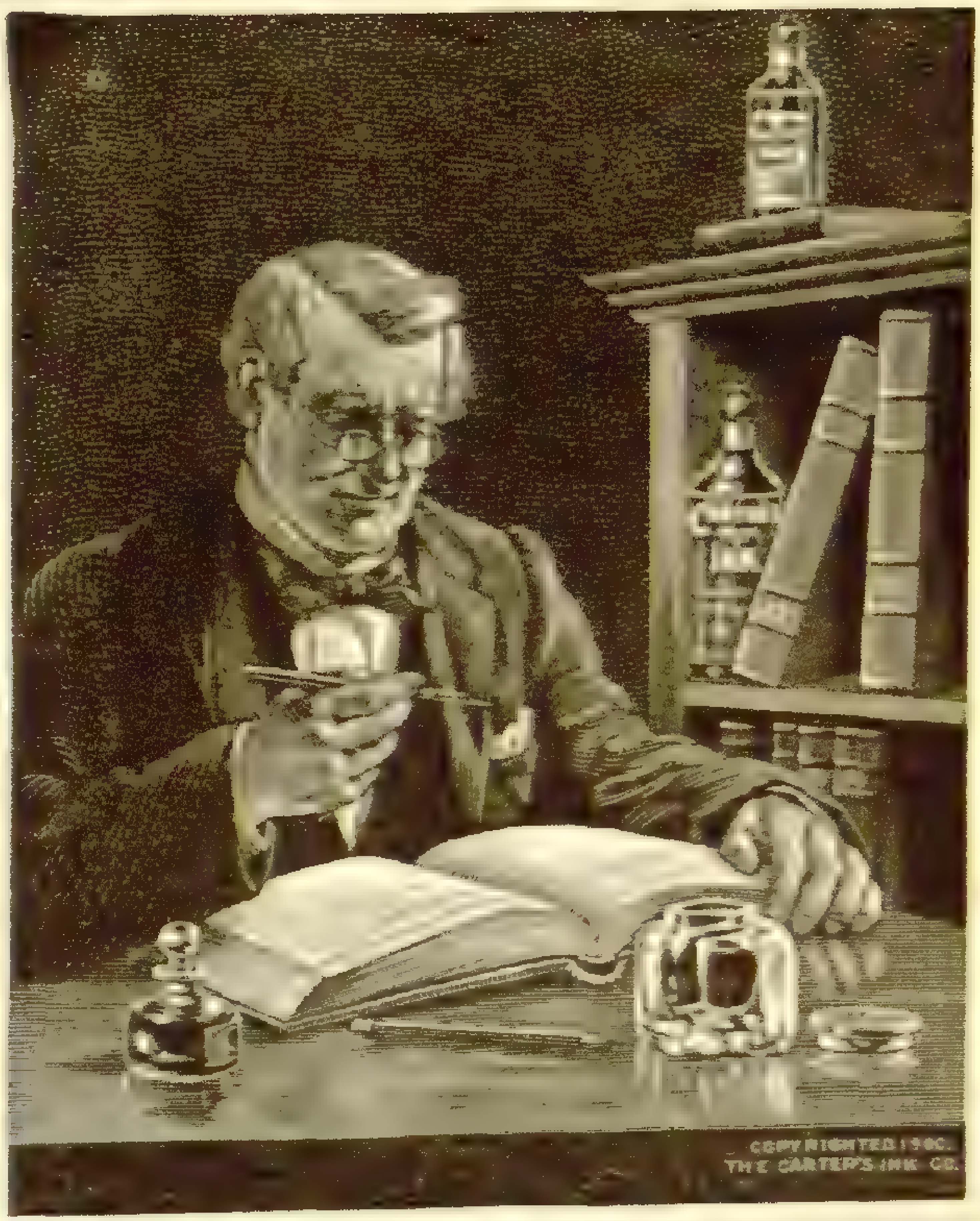

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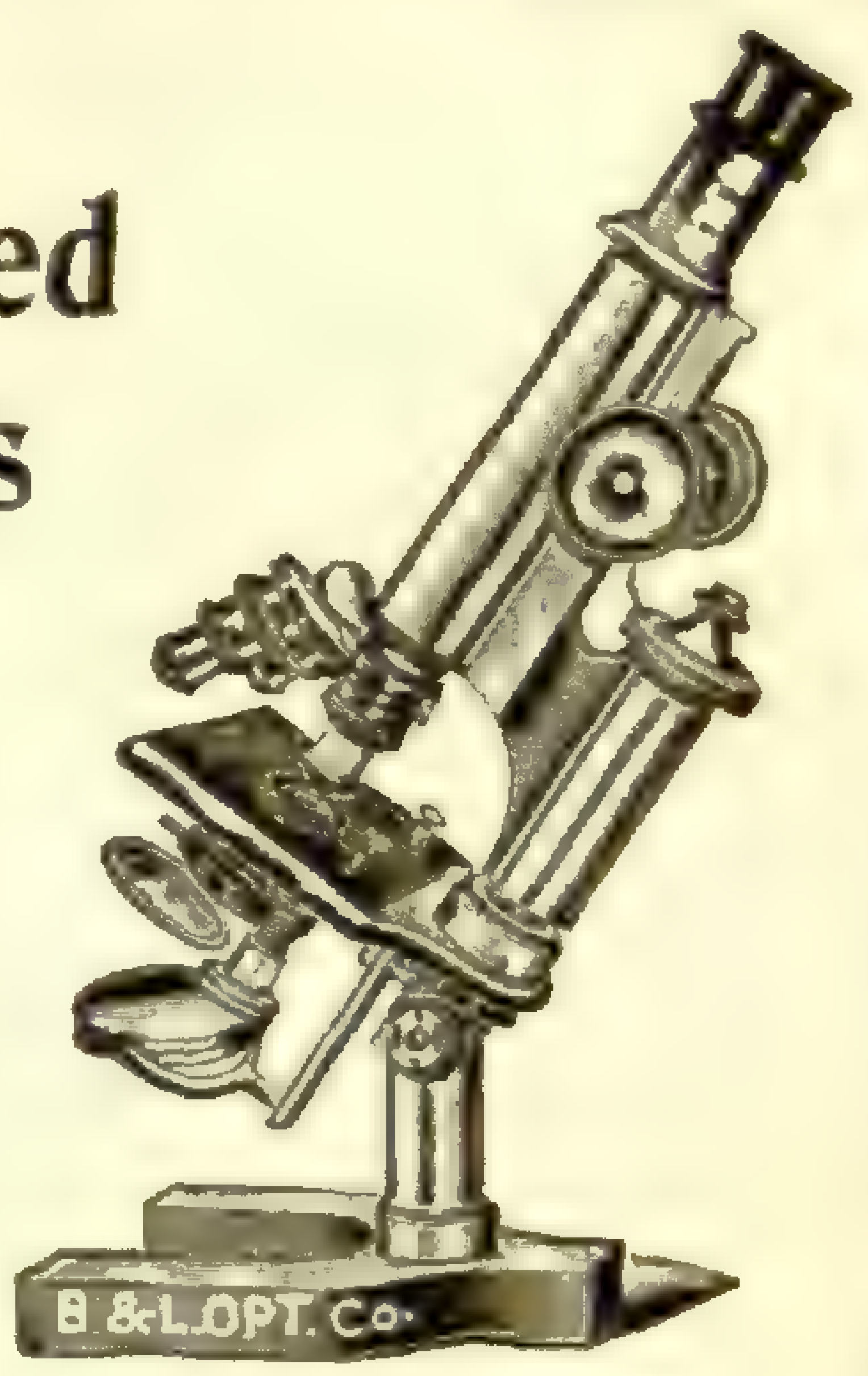

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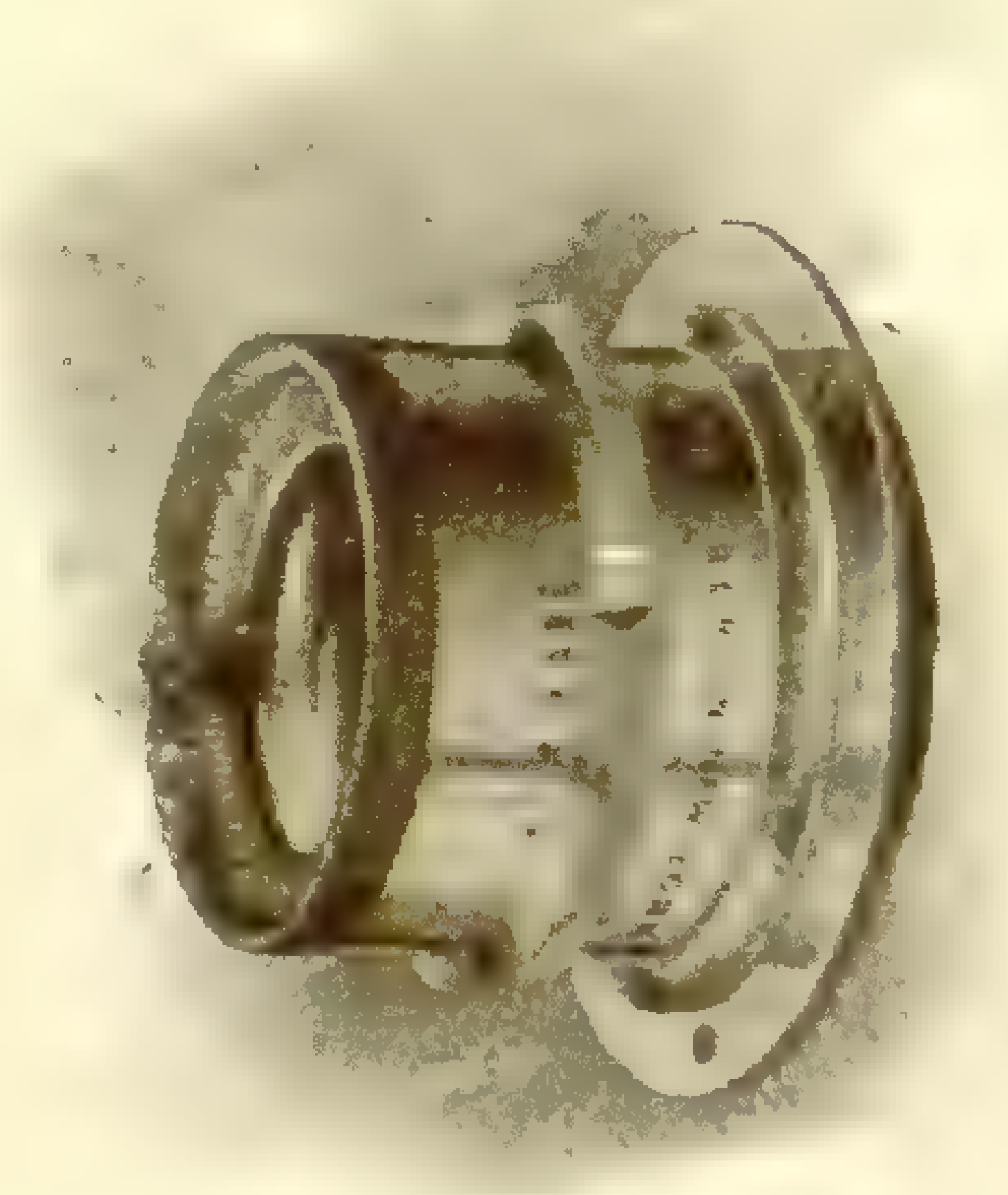

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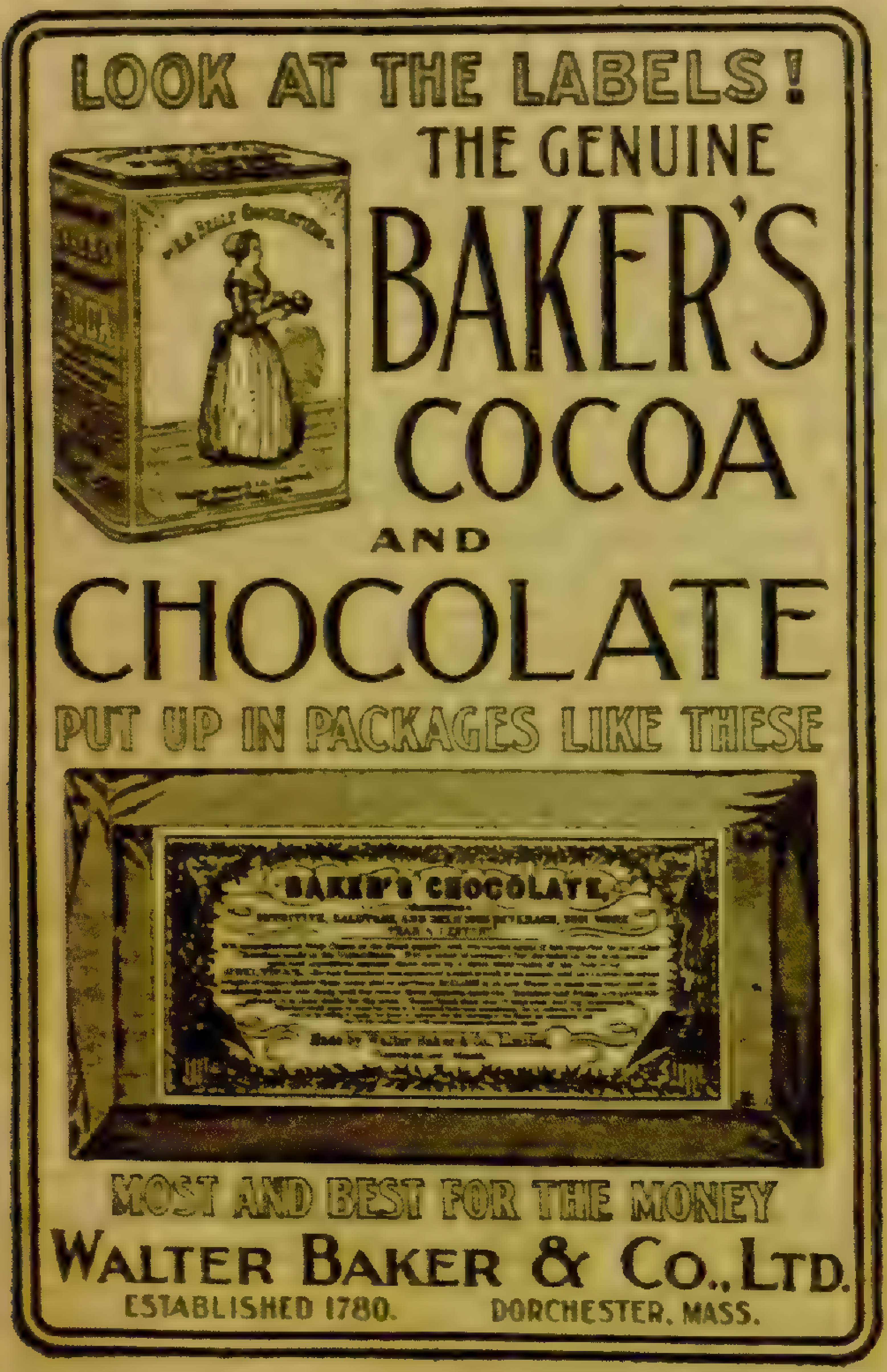

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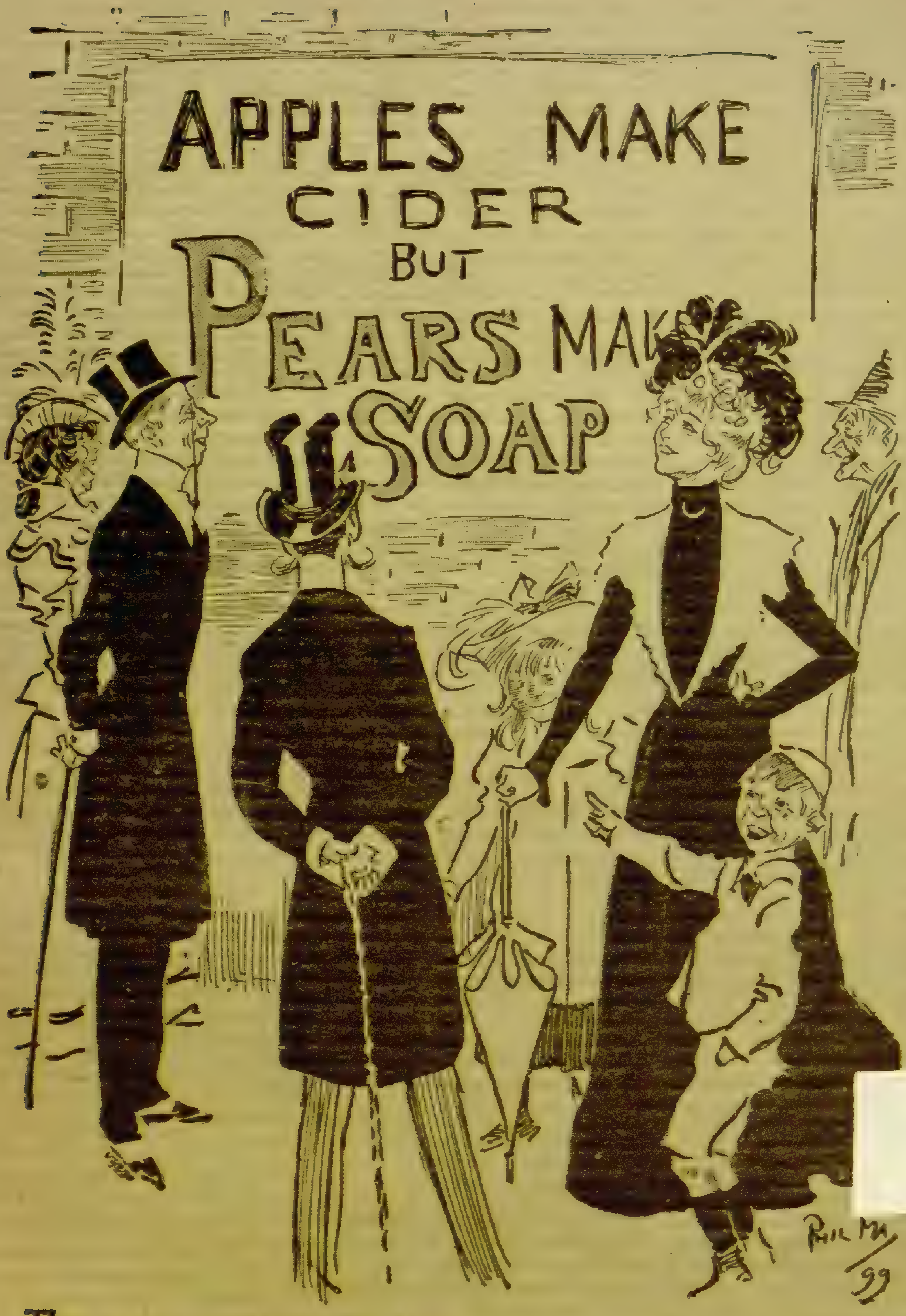
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Vol. XXXII, No. 5 **Issued November 25, 1901**

CONTENTS

NEW OR LITTLE KNOWN UNICELLULAR ALGAE. II.—Eremosphaera viridis and Excentrosphaera. (with plates x–xii) *George Thomas Moore* - - - 309

DEVELOPMENT OF THE POLLEN IN SOME ASCLEPIADACEAE. Contributions from the Hull Botanical Laboratory. XXXII. (with plate xiii) *T. C. Frye* 325

ON THE DISTRIBUTION OF RED COLOR IN VEGETATIVE PARTS IN THE NEW ENGLAND FLORA. *F. Grace Smith* - - - - - - - - 332

SOME PLANT ABNORMALITIES. (with thirty-six figures) *George Harrison Shull* - 343

BRIEFER ARTICLES.

Meissner on Evergreen Needles. (with one figure) *Edwin Bingham Copeland* - 356
The Instability of the Rochester Nomenclature. *M. L. Fernald* - - - 359
Flower Visits of Oligotropic Bees. III. *Charles Robertson* - - - - 367

CURRENT LITERATURE.

BOOK REVIEWS - - - - - - - - - - - 369
Latex and Mucilage
The Flora of Alabama
A Manual of Bacteriology
Methods in Plant Histology

MINOR NOTICES - - - - - - - - - - 373

NOTES FOR STUDENTS - - - - - - - - - 374

NEWS - - - - - - - - - - - - 379

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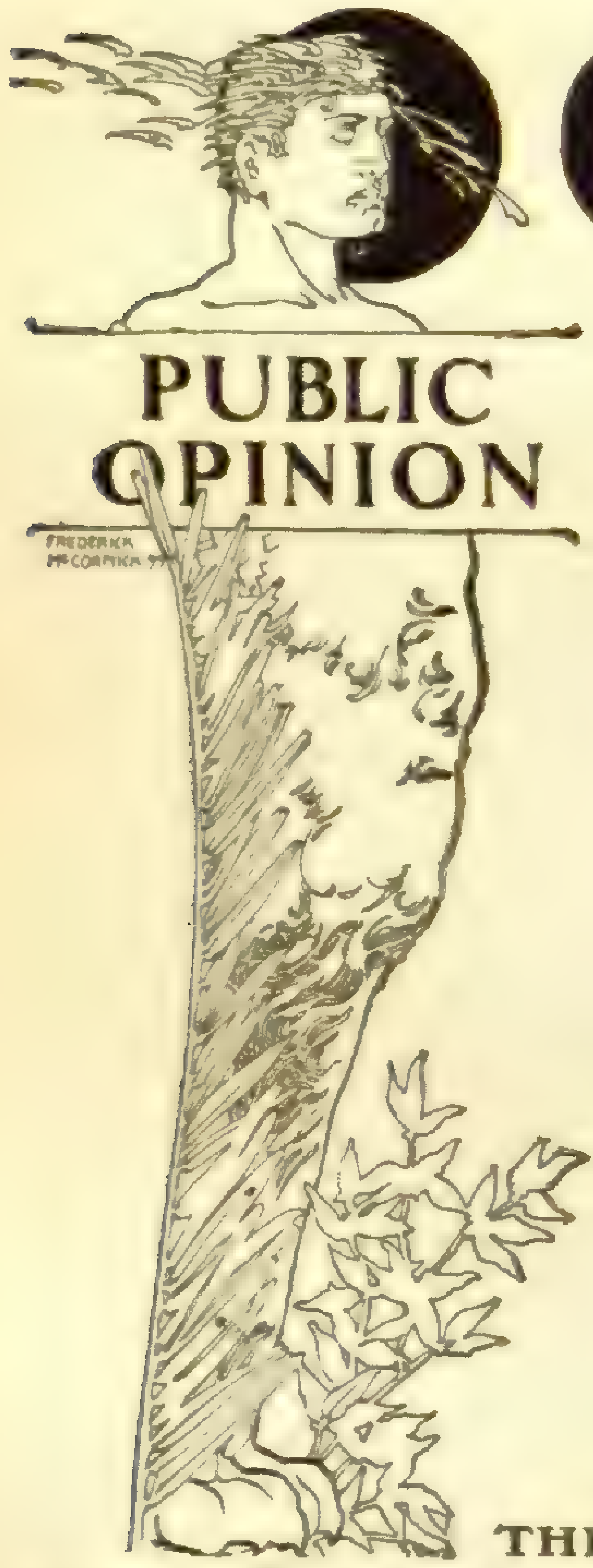

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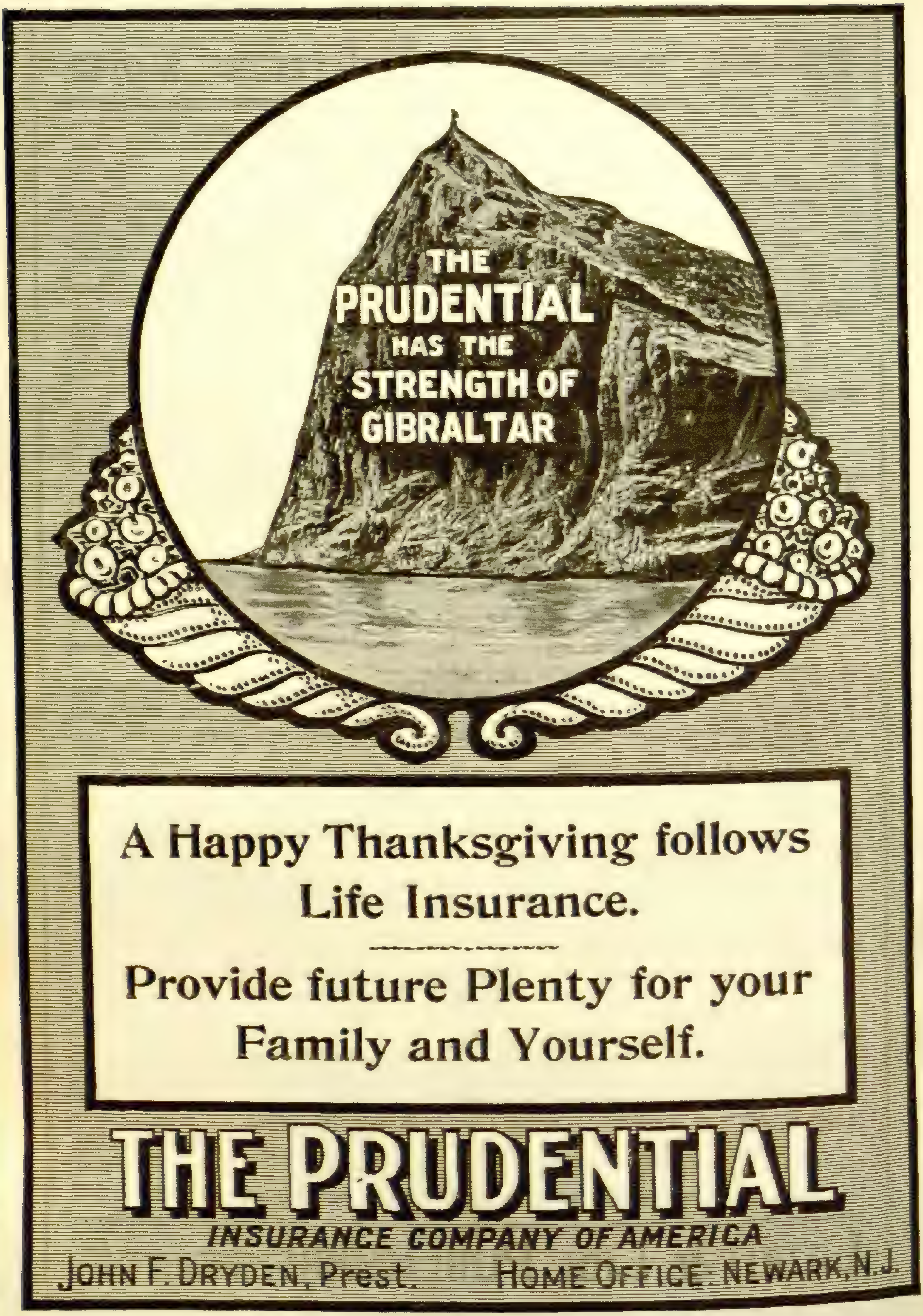

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VOLUME XXXII NUMBER 5

BOTANICAL GAZETTE

NOVEMBER, 1901

NEW OR LITTLE KNOWN UNICELLULAR ALGAE.

II.—EREMOSPHAERA VIRIDIS AND EXCENTROSPHAERA.

GEORGE THOMAS MOORE.

(WITH PLATES X–XII)

Eremosphaera viridis.

AMONG the many algae which have been supposed to represent stages in the life history of other plants, perhaps none have had such a variety of positions ascribed to it as the beautiful spherical form known as *Eremosphaera viridis*. This species was described by De Bary in 1858 in his *Untersuchungen über die Familie der Conjugaten* as a desmid, although he had not observed anything resembling conjugation in the plant, and could only determine its affinities by the mode of division and its general similarity to other well known desmid forms. About the same time, Henfrey (**5**) found this unicellular organism in bogs in Northumberland, and described it as *Chlorosphaera Oliveri*. A good account of the general structure of the plant is given, and because of certain appearances which he assumed to be antheridia, Henfrey says "in the vicinity of Oedogonieae they (Chlorosphaera) will find their true place." Hofmeister (**6**), who described Eremosphaera in his memoir on the Desmidiaceae and Diatomaceae, without giving it a name, regarded it as a link between the Desmidiaceae and Palmelleae.

Twenty-five years later De Wildeman in a measure confirmed the view of De Bary, but stated that Eremosphaera more probably belongs to some developmental stage of a desmid, possibly a zygospore, than represents the vegetative condition of any unicellular alga. More recently De Toni (**3**) describes the genus as an exceedingly doubtful one, suggesting that the large cells resemble fern prothallia, and that we may expect to find it related to the higher cryptogams. Wille (**7**), in Engler and Prantl, places Eremosphaera among the Pleurococcaceae. The last investigator to have had this alga under consideration is Chodat (**1**), who believes that its affinities are such as to put it with the Volvocaceae; furthermore, the results of his observation show a condition of polymorphism which has not hitherto been suggested. In addition to the regular vegetative condition and the ordinary methods of multiplication, which will be described later, Chodat found a number of transition stages which he variously designated as "Gloeocystis" forms, "Palmella" forms, "Schizochlamys" forms, "Centrosphaera" forms, etc. According to Chodat, these various stages of Eremosphaera are actually the same thing as the genera which they resemble, and we can no longer recognize them as distinct species, but must include them all under the single name *Eremosphaera viridis*. It was with the desire to clear up the question as to the polymorphism of this form, and to settle, if possible, its life history and affinities, that the investigation concerning this alga was undertaken.

MATERIAL.

The specimens first studied were secured from a small pool formed by a sluggish brook running through a marsh near Ridge hill, Mass. Although the pool is quite small, there is usually plenty of water, and at no time during the year is the material absent from this locality. There was no sphagnum growing in the pool, as seems usually to be the case where Eremosphaera is found, but an abundance of Zygnema, Spirogyra, and other Conjugatae, notably Micrasterias, was frequently present. The plants were first discovered in May 1897, when they numbered about twenty to the cubic centimeter. Since that time they have been collected during almost every month of the year, always in considerable quantities.

In August, 1899, while on Naushon, one of the Elizabeth islands, near the place on the east shore known as Tarpaulin cove, Eremosphaera was found in its typical habitat, namely a low sphagnum swamp. There was practically no difference between the forms from the two localities except that of size, and this was quite characteristic. Out of the two hundred and fifty measurements of the specimens from Ridge hill (*fig. 1*), the average diameter was 75.45μ with a maximum of 105μ and a minimum of 67.5μ; while of the same number of spheres from Naushon (*fig. 3*) the average diameter was but 35μ with a minimum of 31.5μ and a maximum of 40.7μ. The figures above referred to will give a fair idea of the comparative sizes of the two lots of material.

This marked difference in size has been noticed by Chodat (1), who in the spring of 1892 found Eremosphaera which was almost exclusively the large form, while in 1894 he discovered among Sphagnum and Carex a quantity of the small variety. The relative sizes of these two extremes is not given, except for the statement that by careful search one might find "giant individuals" of 170μ. De Bary, in his original notice of the plant, gave the measurements as about 60μ, while Rabenhorst says 43–49μ. Kischner gives 100–145μ, and De Toni covers both extremes by citing 100–150μ, as the usual size, 30–80μ specimens being occasionally found. It is evident, then, that the plant is one varying within wide limits. The maximum of the Naushon form not coming within 26μ of the minimum of the Ridge hill form, if size be a sufficient criterion there would be no difficulty in recognizing a variety *minor*, measuring from 30–41μ, and a variety *major*, measuring from 67–100 or more microns. There can be no question that the smaller forms, found by me at Tarpaulin cove, were mature plants. The arrangement of the chromatophores and general cell contents was in every way identical with the larger forms, and division took place as readily in cells 33μ in diameter as in those measuring 100μ. Furthermore, cultures grown from material from the two localities have retained their characteristic size through a cultivation of more than eighteen months in one case, and for over three years in the other.

GENERAL STRUCTURE.

In appearance Eremosphaera resembles a perfect gelatinous sphere with numerous minute chromatophores usually lining the wall. The arrangement of the chromataphores varies greatly, hardly any two specimens showing exactly the same pattern. Usually they are scattered about in an irregular fashion, sometimes singly, sometimes in groups (*fig. 1*); or they may radiate from the center in a quite definite manner (*fig. 10*). That light has much to do with the arrangement of the color-bodies may be seen from *fig. 4*. This specimen while kept in subdued light showed a cell of almost solid green hue, so thickly were the chromataphores lining the wall. After five minutes in bright sunlight, however, the condition shown in *fig. 4* was obtained, and in watching the effect under the microscope the chromatophores could be seen sliding along the protoplasmic strands which radiated from the centrally placed nucleus.

When the chromatophores are at the periphery of the sphere and are not too great in number, the nucleus is easily recognized without the aid of stains. The method recommended by Chodat (1) of clearing with chloral solution and staining with carmine brings it out well, and also reveals one or more nucleoli (*fig. 2*). At times the nucleus and the protoplasmic mass surrounding it become quite granular, giving the appearance of some foreign body within the cell. The strands which radiate from the nucleus connect with the protoplasm lining the cell wall and form quite a complete network (*fig. 5*).

The chromatophores are irregular both as to outline and as to size, varying from circular, through broadly elliptical, to narrow fusiform (*fig. 16*). Occasionally they are angular, of a rhomboidal outline, a type especially common in the variety *minor*. The honeycomb appearance described by Chodat (1) was not visible in my material, neither was the platelike expansion which he says is drawn out from the middle of the chromatophore and may consist of two or three bent wings, causing an irregularly shaped dark spot in its center. A good sized pyrenoid is always distinctly visible, there being sometimes as many as three or four in each chromatophore. If the chromatophore be treated after the manner of Mayer, first adding a dilute iodine solution and then chloral hydrate, the crystalline structure of the pyrenoid is easily seen (*fig. 18*), and the layer of starch surrounding it made visible.

The wall of Eremosphaera is normally thin and of but a single layer in thickness, but it has the property of great gelatinization, and is often laid down in successive layers. This condition gives rise to the forms characterized by Chodat as the Gloeocystis, Palmella, and Schizochlamys stages. The duplication of the wall does not seem to be confined to particular periods of development, but may occur at any time. Each wall soon becomes separate and distinct from the adjoining ones, and with care the several coats may be broken one at a time and the contents allowed to slip out. That such forms are really what botanists recognize as Gloeocystis or Schizochlamys is doubtful. While it is possible that Emerosphaera, surrounded by a number of gelatinous walls, might be mistaken by a hasty observer for a similar condition in either Gloeocystis or Schizochlamys, it does not necessarily follow that these genera are one and the same thing. Schizochlamys, I have been able to cultivate for a considerable length of time, and it has never exhibited any evidence of being related to Eremosphaera. Since we can have the same duplication of the wall in Chlamydomonas and other genera widely separated from the ones under discussion, it hardly seems a sufficient basis upon which to unite a number of forms frequently showing marked differences in their life histories.

In addition to the successive formation of coats around Eremosphaera, there sometimes occur peculiar growths on the inner surface of the wall, which are the result of a number of layers of cellulose being formed about a central point (*fig. 11*).

These concentric layers can occasionally be separated by crushing, but usually they are very compact. They project inward towards the center of the cell, and in case a second continuous wall is formed, it remains indented wherever these excrescences appear. As many as twelve secondary walls have been counted around a single sphere, and there seems to be no limit to their formation.

CULTURE METHODS.

A plant which has had as many developmental stages ascribed to it as Eremosphaera naturally necessitates the most careful application of pure culture methods. Consequently the cultivation of this plant was attempted as soon as it was procured, and cultures have been kept running successfully for about three years. As it was not convenient to visit the original locality frequently, and to obtain fresh material in that way, it seemed best to maintain a number of gross cultures from which pure transfers might be made at any time. No trouble was experienced in this, and water from the original pool, containing diatoms, numerous filamentous algae, and Eremosphaera, has been kept continuously in the laboratory. Bacteria appeared for a short time, but the water soon cleared, and all the algae have maintained themselves in good condition. These gross cultures were kept either in crystallizing dishes or wide-mouthed bottles, over which was a sheet of glass to prevent too rapid evaporation. It was found that the crystallizing dish was most convenient for this purpose because of the ease with which material could be picked out from it. The large Eremosphaera cells were readily found with a hand lens, and then transferred by means of a pipette to a watch glass. Here they were washed several times in sterilized water, and then examined under the microscope, before being placed on the culture medium.

Various methods of cultivation were tried. The well-known solution of Knop was used in strengths from 0.2 per cent. up to 1 per cent., both as a fluid culture and in connection with agar agar and gelatin. The gelatin was soon abandoned, however, on account of the low temperature at which it liquefied, since agar agar (5 to 7 grams to the liter of nutrient solution) enabled one to keep perfect trace of the cells, and was more satisfactory for many reasons. Stender dishes were used for culture vessels because it was desirable to have as large an amount of the medium as possible, so that the cultures would last for some time, and in order that there might be a considerable surface for growth. The same precautions of sterilization were observed that would have been necessary for bacteriological work, and check cultures indicated that these methods were successful.

Usually after sterilization there would be a considerable amount of moisture collected upon the surface of the agar, and it was in this fluid that the Eremosphaera cells were deposited. If placed directly upon the surface of the agar it seemed impossible for them to persist, but when transferred to the moisture and then gradually, through the evaporation of the superfluous liquid, brought in contact with the nutrient agar there was no difficulty in making them grow as well as in fluid media.

Van Tieghem cell methods were not successful. The plants lived for a considerable length of time and the chlorophyll granules moved under the influence of sunlight, but there was no development of any kind. Cultures kept in tightly sealed cells for several months would gradually present an appearance resembling the formation of spores, and at first this was thought to be the case. Upon investigation, however, it was found that this effect was due entirely to the rounding off of the chromatophores, which were closely packed at the periphery of the sphere. Upon being restored to natural conditions such cells resumed the characteristic arrangement of the color bodies, and the nucleus at no time presented any other appearance than that found in the normal plant.

Ward cells, which allowed a constant supply of air and yet prevented any contamination from the outside, were partially successful. The most satisfactory method for making direct observations of cultures, however, was to isolate a single individual and place it on a slide either in sterilized water or a nutrient solution. A large cover-glass was then placed over it, being propped up by three or four minute drops of a mixture of beeswax and vaseline. A bell jar lined with moist filter paper was sufficient to prevent the evaporation of the solution for twenty-four hours, and a drop of nutrient fluid added at one side of the cover-glass replaced any loss during the examination under the microscope. Such cultures require daily examination, of course, but when the life history of an organism is being followed out this is an advantage rather than an objection. The wax supports for the cover-glass were preferable to bits of glass or filter paper because they permitted the crushing out of a specimen, if necessary, and held the cell in just the desired position. Cultures of this kind gave the best of results, the algae apparently developing in a perfectly normal manner.

MULTIPLICATON AND DEVELOPMENT.

De Bary, in his observations upon Eremosphaera, discovered that it multiplied by simple division into two or four cells, each of which soon attained the size of the original plant. Henfrey likewise recognized this condition. Such a division is accomplished by the formation of a new wall between the two halves of the original cell. This wall extends completely around each half, and as the nucleus divides and the chromatophores, with the protoplasm, form into two irregular masses, the gelatinous wall pushes in from the periphery, forming the division (*fig. 6*). The two cells thus formed gradually increase in size, so that in a short time the original wall is ruptured and the daughter plants are liberated. These usually escape as perfect spheres, but may retain their flattened appearance for a short time, as is shown in *fig. 7*. More rarely a second division may take place at right angles to the first, thus producing four daughter cells instead of two (*fig. 8*). Wolle (8) and Chodat (1) both speak of even further successive divisions, but my material has never shown more than four cells formed in this way.

This method of simple division has been believed to be the only means of propagation in Eremosphaera, and it was not until the result of the researches of Chodat became known, that a more complicated life history, including the formation of zoospores, was suspected. Henfrey, in his discussion of the plant already referred to, suggested the possibility of antherozoids, but this condition was undoubtedly due to the presence of some parasite, which Henfrey himself recognized as a possible cause.

While considerable doubt has been cast upon Chodat's interpretation of what he saw, the fact that certain of the stages which he describes certainly exist in material found in this country, makes it necessary that a most careful search be made for all the forms supposed by him to be connected with Eremosphaera. In addition to the well-known division into two or four spheres, Chodat (1) describes a kind of sporangium-building condition where division goes on until the diameter of the ultimate cells is ten to twenty times smaller than at first. This stage I have been unable to find, and nothing of the sort seems to occur in the material I studied, either in gross or pure cultures. In addition to these non-motile spores, Chodat describes ciliated spores. Just how and when these may be formed is not clear, but it is to be inferred that they arise from some "palmella" condition and not directly from the adult plant. These zoospores, according to Chodat, are usually elliptical, and are always surrounded by a gelatinous coat, reminding one of certain forms of Chlamydomonas. Each zoospore has a red eye spot, a radiating chromatophore, and an evident nucleus. In most cases there are two cilia, but exceptionally three. The question as to whether they actually had four remained undecided, as did also the possibility of their conjugation. They seem to have been irregular both as to size and shape, for Chodat (1) says, "da ihre Mutterzellen an Grosse sehr verschieden sein konnen, so sind infolgedessen die Zoosporen auch sehr verschieden, sowohl was die Grosse als auch die Form anbetrifft."

Although a most careful search has been made among material growing under all conditions, not the slightest trace has ever been discovered of any motile spore in evident relation to Eremosphaera. Occasionally plants would be found of a lighter green color, filled with spherical bodies (*fig. 13*), which in general resembled a sporangium. But while these cells were observed daily for weeks they not only failed to show any signs of further development, but gradually disintegrated instead. After having observed algae which were crushed and noting the manner in which the chromatophores formed a colorless membrane about themselves, with the green collecting at one side, as in *fig. 17*, it would seem almost certain that the conditions I had been observing were due to injury, and the admission of a small amount of water caused the abnormal appearance suggesting spores. On one occasion, a plant of this sort showed four or five biciliate organisms within it, which at first were supposed to be zoospores (*fig. 14*). Their subsequent development (*fig. 15*), however, proved them to have no connection with the alga, and after three days, when the culture was crushed out, it was found that the organisms possessed no chlorophyll, a fact which could not be made clear with certainty while they were embedded among the chromatophores.

Failing to find zoospores under natural conditions, it was hoped that some change in the environment might be produced which would cause zoospore formation. Plants, closely encysted in numerous gelatinous coats and which had been growing in a nutrient solution, were removed to fresh water and to variously modified media. Some cultures were allowed to remain in the sunlight, others were kept in darkness. Specimens taken direct from nature were placed in numerous solutions and subjected to all possible changes of temperature and moisture. Aeration was tried for lengths of time varying from a few hours to several weeks, and cells were kept on ice over night, and then gradually brought into the temperature of the laboratory. But none of these methods yielded any thing more than the previously described method of division. Consequently, after having had cultures running for over three years, and making repeated examinations of material collected under natural conditions, it must be said that at no time was there any appearance which gave the slightest evidence of zoospore formation, and it is certain that in the forms found growing in this country zoospores must be very rarely, if ever, formed.

The rejuvenescence described by Chodat (1), wherein a cell instead of dividing simply slips out from the old sheath, was frequently seen and is represented in *fig. 5*. Whether this can really be termed a rejuvenescence, according to the ordinary use of the term, is a question. It seems as though this condition can hardly be different from those which show a succession of walls, except that in the first case the outer wall is not strong enough to hold the cell, and it slips out as indicated. There never appears to be any change in the contents of the cell, not even in the arrangement of the chromatophores.

In the mud at the bottom of the water containing Eremosphaera, there will usually be found a considerable number of resting cells. These are of the typical brick-red color, and generally show successive layers of sheaths. They contain large quantities of oil, and in no way appear to differ from the same type of spore in other algae. So far as observed, the development of the resting spore was not accompanied by the formation of any new cells. The red color was gradually lost, the chromatophores became more and more prominent, and the normal vegetative appearance of Eremosphaera was the result. Usually the resulting cell is quite large and division takes place in a very short time. No division of the resting spores was observed, the condition indicated in *fig. 19* being an example of where two cells passed into the resting condition almost immediately after division, and before they had time to enlarge. This is not an infrequent occurrence.

TAXONOMIC POSITION.

It is evident from the foregoing that there is no reason for supposing that Eremosphaera is related to the desmids or to any of the Conjugatae; neither does it seem possible to show that it forms any part of the life history of any of the higher cryptogams. The theories of Henfrey (5) and Hofmeister (6) may also be dismissed, so that there only remain the two positions ascribed to it by Chodat (1) and Wille (7). Chodat, as the result of his study of Eremosphaera, came to the conclusion that it had evident affinities with the Volvocaceae, and if all the stages described by him are really passed through by this plant, it would seem as though some such disposition would have to be made of it. On the other hand, the negative results of my cultures and observations would seem to throw some doubt upon its supposed polymorphism, particularly with regard to a motile stage. It seems, therefore, that for the present at least, Eremosphaera should be classed with the group of green algae possessing no zoospores, namely the Protococcoideae.

Excentrosphaera, nov. gen.

There still remains to be discussed the form described by Chodat as the "Centrosphaera" stage. This form was present in small quantities in the first material collected at Ridge hill, and was immediately separated from the Eremosphaera cells and cultivated. The growth was luxurious in fluid nutrient media, and satisfactory, if not so abundant, on agar. In addition to these pure cultures, a number of dishes containing water from the pool which supplied the original material were kept in the laboratory, and in the course of a few months became filled with a large number of these plants. The conditions for growth under these various circumstances seemed favorable and normal, but there was at no time any evidence of the slightest connection with the developmental history of Eremosphaera. After having had this form under cultivation for about three years, and having seen it pass through its life cycle over and over without assuming a stage which in any way resembled those of Eremosphaera, I am obliged to conclude that it is an independent genus. Since it does not seem to have been described elsewhere, the name *Excentrosphaera viridis* has been given to this alga.

Excentrosphaera, in its mature condition, may assume an outline varying from that of a perfect circle, through all gradations to an ellipse, as well as occasional excentric and indefinite shapes. The general resemblance to the forms assumed by germinating

Ulothrix spores is striking, but the much larger size, the arrangement of the chromatophores, and suosequent development make it an easy matter to differentiate this plant from that genus.

The numerous large chromatophores are crowded near the surface of the cell, and are usually arranged radially (*figs. 21, 23, 24*). As the cells assume irregular shapes the chromatophores may be distributed in various ways, and there are often lacunae between the chlorophyll masses. Sometimes there are several layers of chromatophores, so that except for the nucleus and a small amount of protoplasm, the cell is almost filled with these bodies. There are numerous minute pyrenoids in each chromatophore, but these are not readily made out without the use of stains. The densely packed chromatophores render it difficult to see the centrally placed nucleus, with its nucleolus, but sections (*fig. 25*) or crushing will usually reveal it. When the cells are about to form spores the nucleus divides repeatedly (*fig. 26*), then the chromatophores break up, and in a short time the entire cell has a homogeneous appearance similar to that shown in *fig. 27*. The spores, which are formed from this condition simultaneously, are 2–3μ in diameter, non-motile, and without a red spot. They escape through a hole formed by the dissolution of the wall (*fig. 22*), and in about a month increase to the size of the mature plants. The developing spore usually remains spherical until it has reached its maximum size, and not until then does it begin to take on the irregular shape previously referred to.

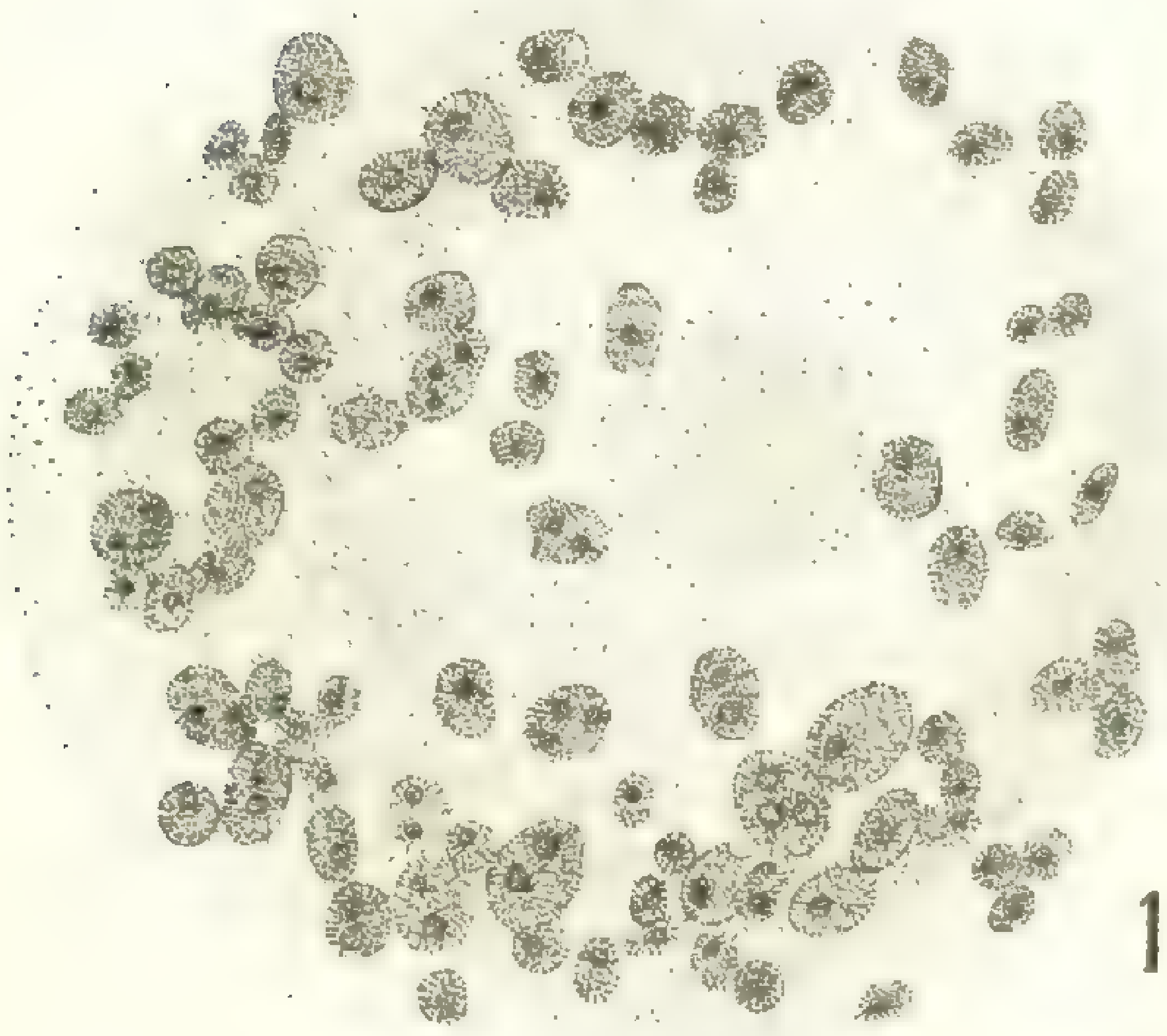
The wartlike projections on the wall, reported by Chodat (1), frequently occur in plants after maturity has been reached, but in small spherical forms are quite rare. These formations are made up of a series of layers of cellulose, and often increase until they are of considerable size (*figs. 23, 24*).

Resting conditions, with a very thick wall and of a reddish color, were found in pure cultures, but the mode of development has not been observed up to the present time. As previously stated, this plant has been cultivated in a pure state for several years, and all the methods resorted to in an effort to bring about zoospore formation in Eremosphaera were repeated with Excentrosphaera, but without success.

The Eremosphaera material found on Naushon has never shown Excentrosphaera, nor has the Ridge hill material developed it after the original lot was collected. Excentrosphaera has been found in stagnant ponds near Norwich, Vt., which contained, in addition, large amounts of Nitella, Spirogyra, Oedogonium, and related forms. A shallow pool, almost filled with Hydrodictyon, not far from Boston, has also furnished Excentrosphaera in considerable quantities. Neither of these latter localities have ever shown Eremosphaera, although repeated search has been made for it. Unless we are to adopt Borzi's "stadii anamorphici" for all the algae, it does not seem possible that this plant has any genetic connection with any other form. The external resemblance to Centrosphaera, which led Chodat to give that name to it as a supposed stage of Eremosphaera, is certainly striking, but the decided difference in habitat, together with the absence of motile spores and the difference in development, would seem to be sufficient to separate it from that genus. The affinities of Excentrosphaera, so far as known, must be with the Protococcaceae of Wille.

Excentrosphaera, nov. gen.—Plant consisting of a single cell, in mature condition varying in outline from spherical and elliptical to irregular and excentric forms. Chromatophores large, angular, usually radiately arranged, closely lining the wall. Pyrenoids minute, numerous in each chromatophore. Multiplication by means of non-motile spores (aplanospores), which escape by the dissolution of a part of the cell wall. Reaction to all external stimuli negative.

E. viridis, nov. sp.—*Plate XII, figs. 21–27.* Characters of the genus. Plants of bright green color; size of mature cells 22–55μ. Spores 2–3μ. Growing with Eremosphaera, Geneva (?); with Eremosphaera, Micrasterias, Zygnema, etc., Ridge hill, Mass., the year around; in swamps with Nitella and various algae, Norwich, Vt., September–November; with Hydrodictyon in shallow pool, in vicinity of Boston, June–August.



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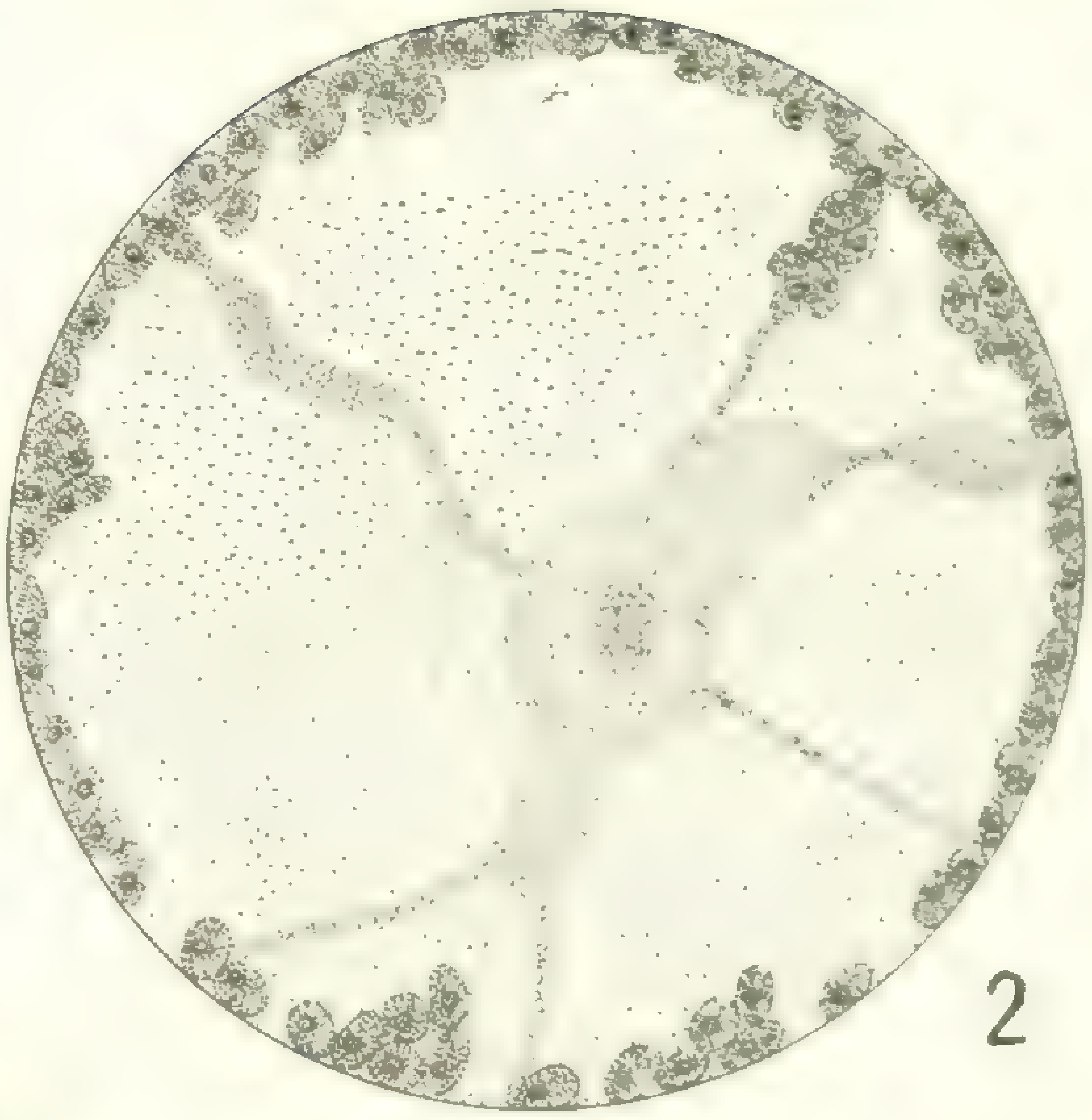

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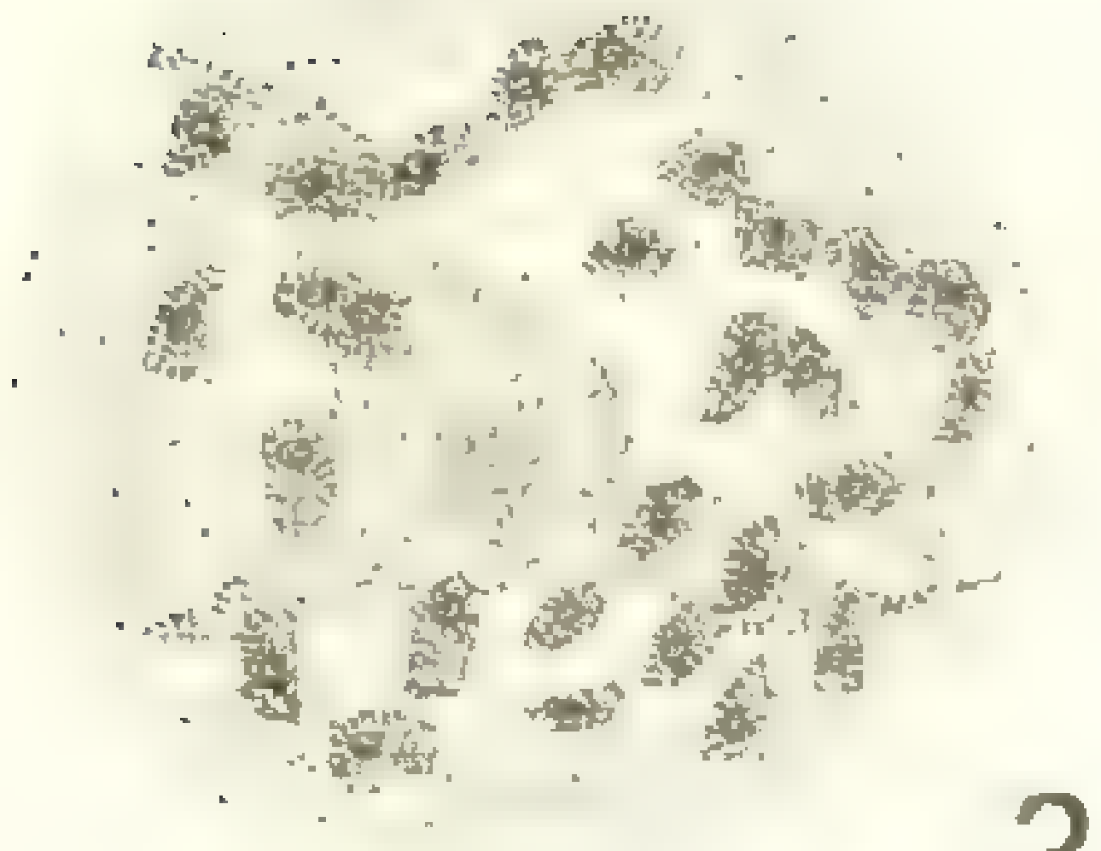

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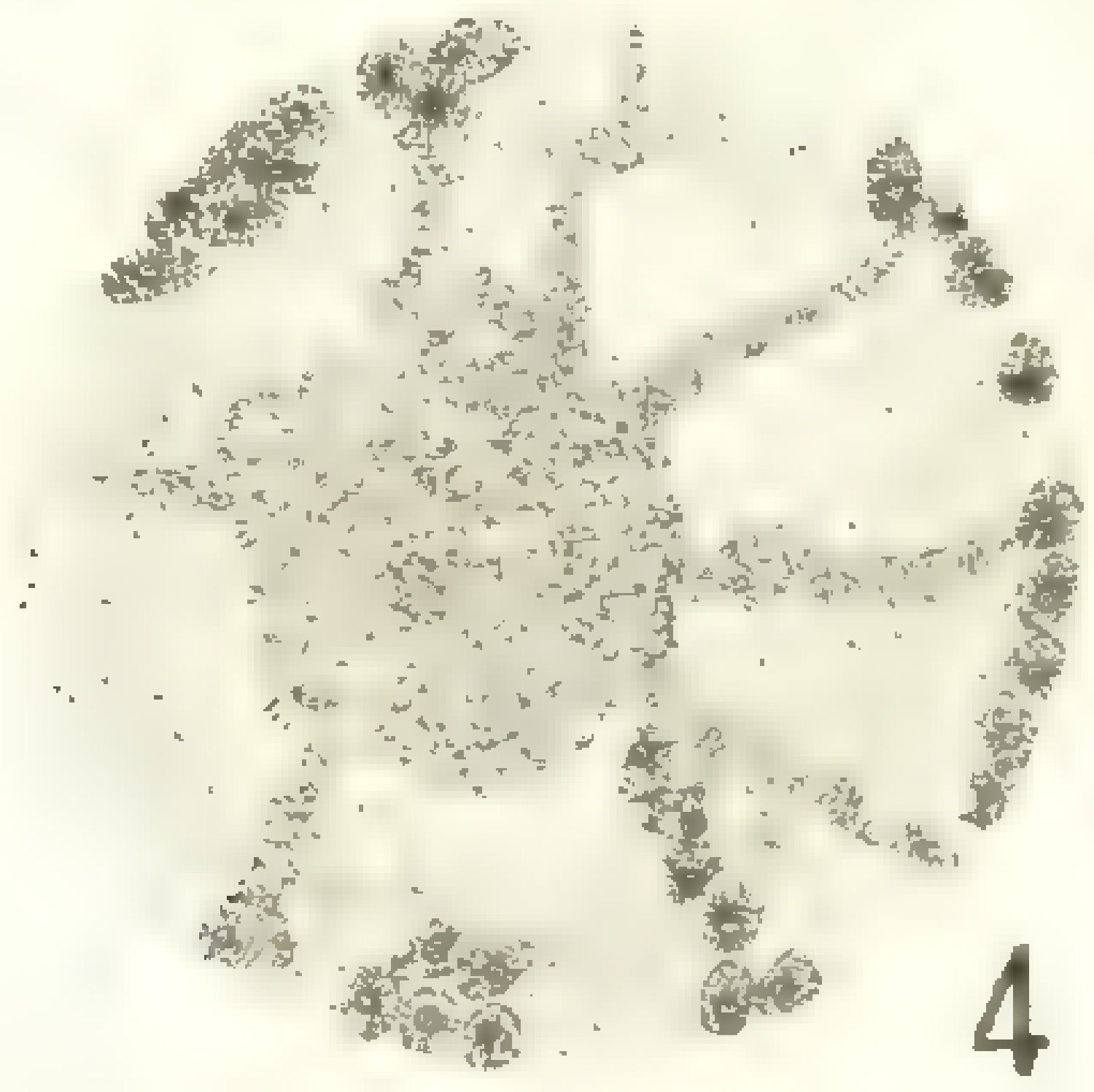

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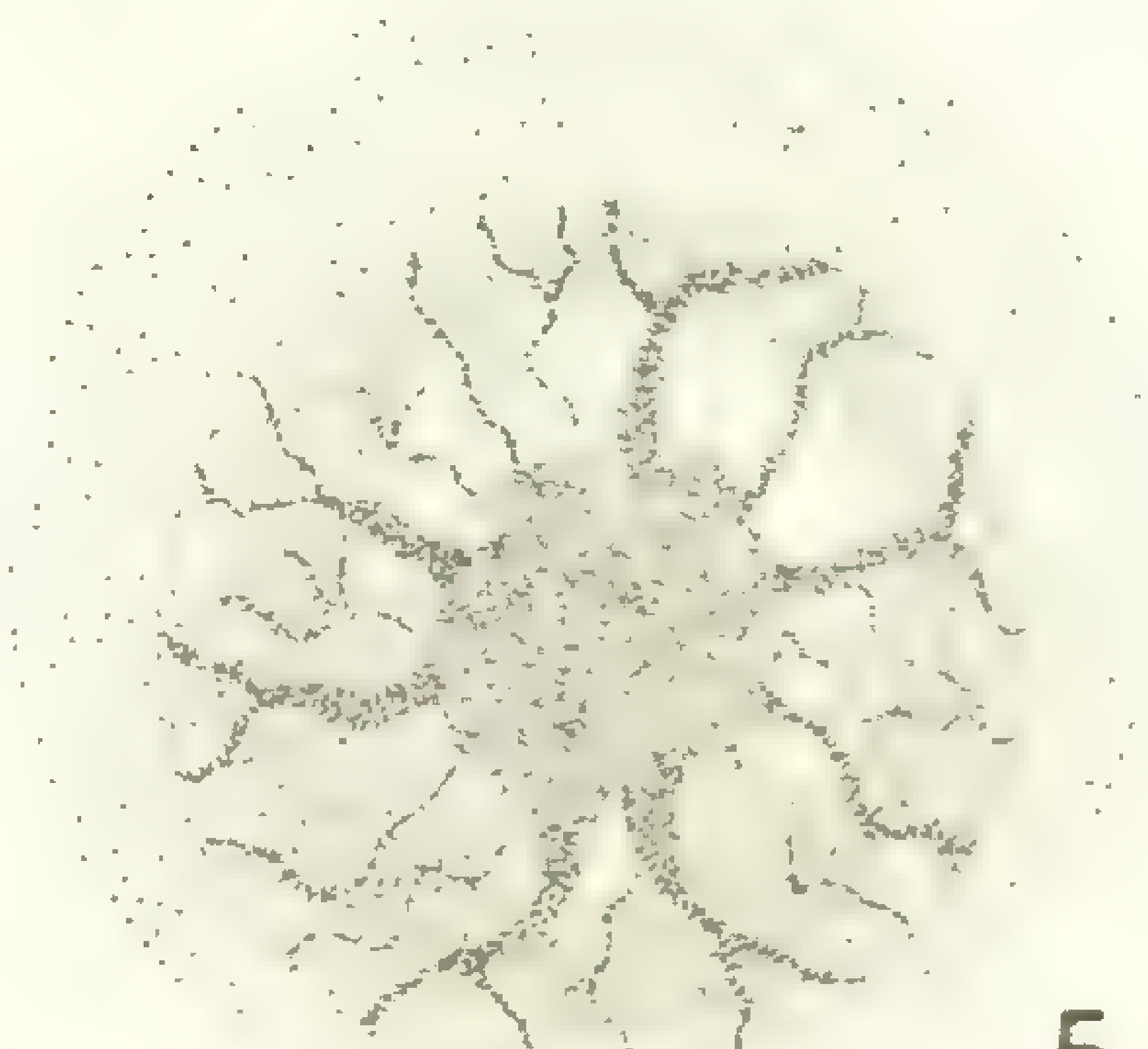

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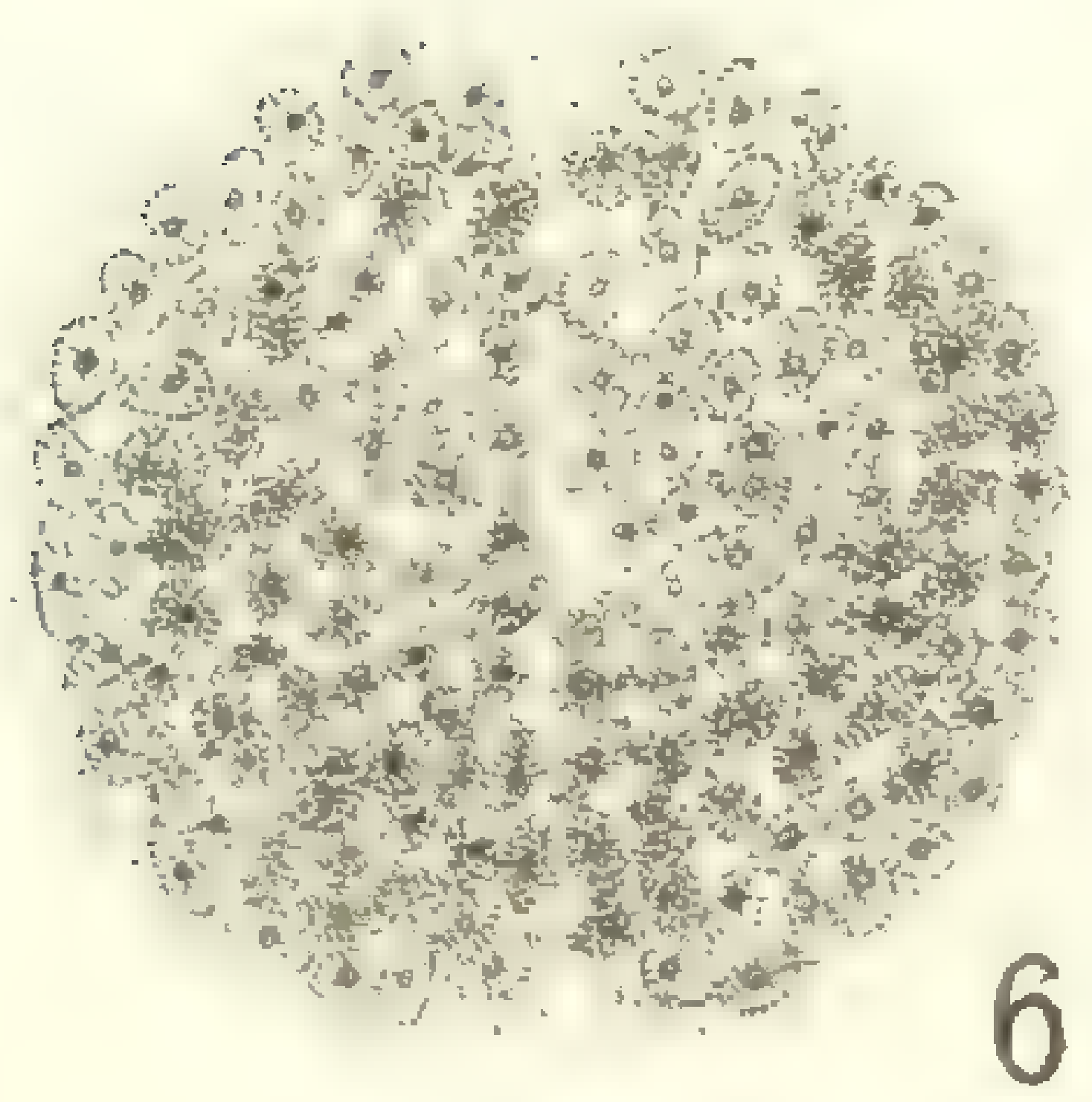

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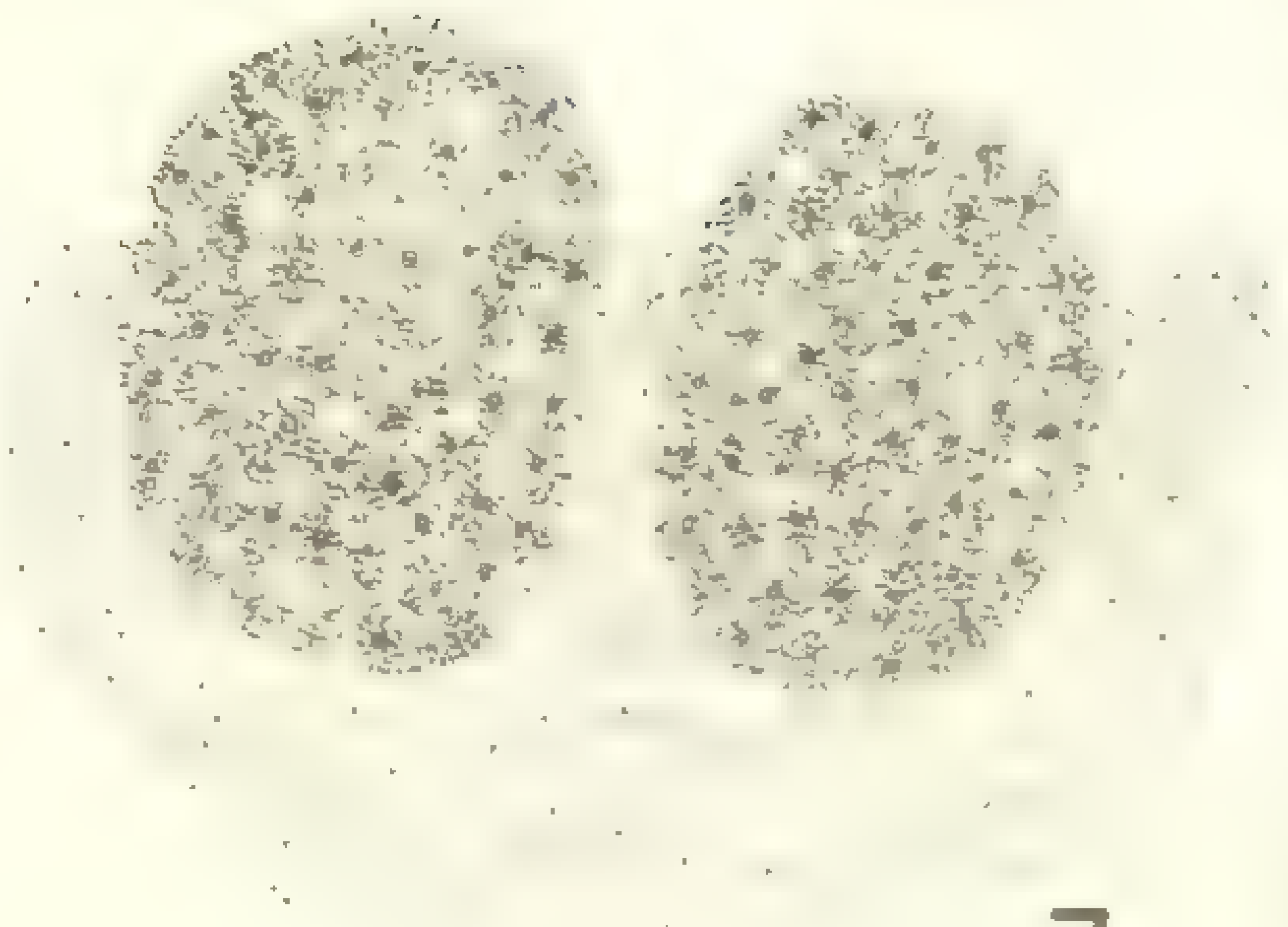

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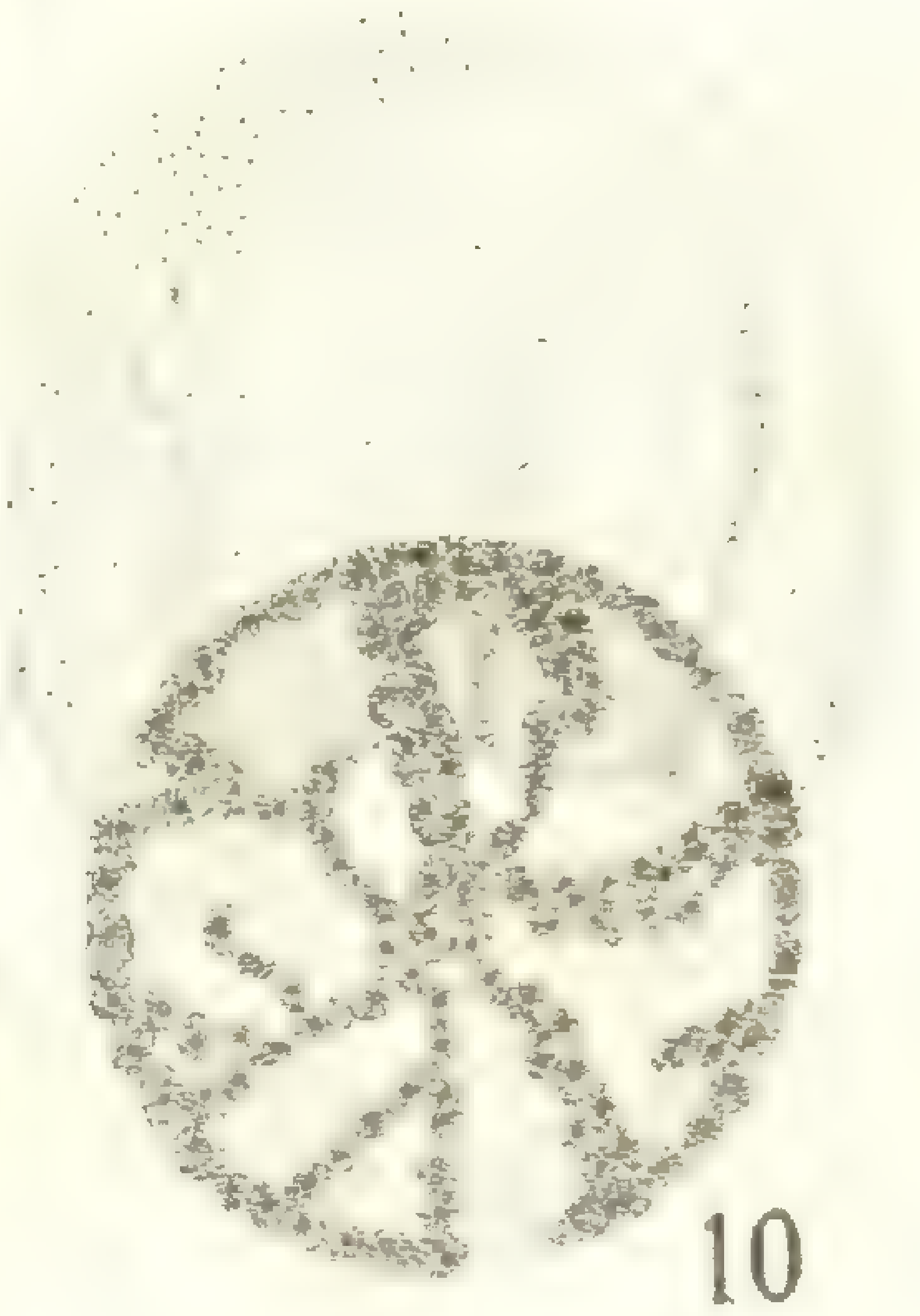

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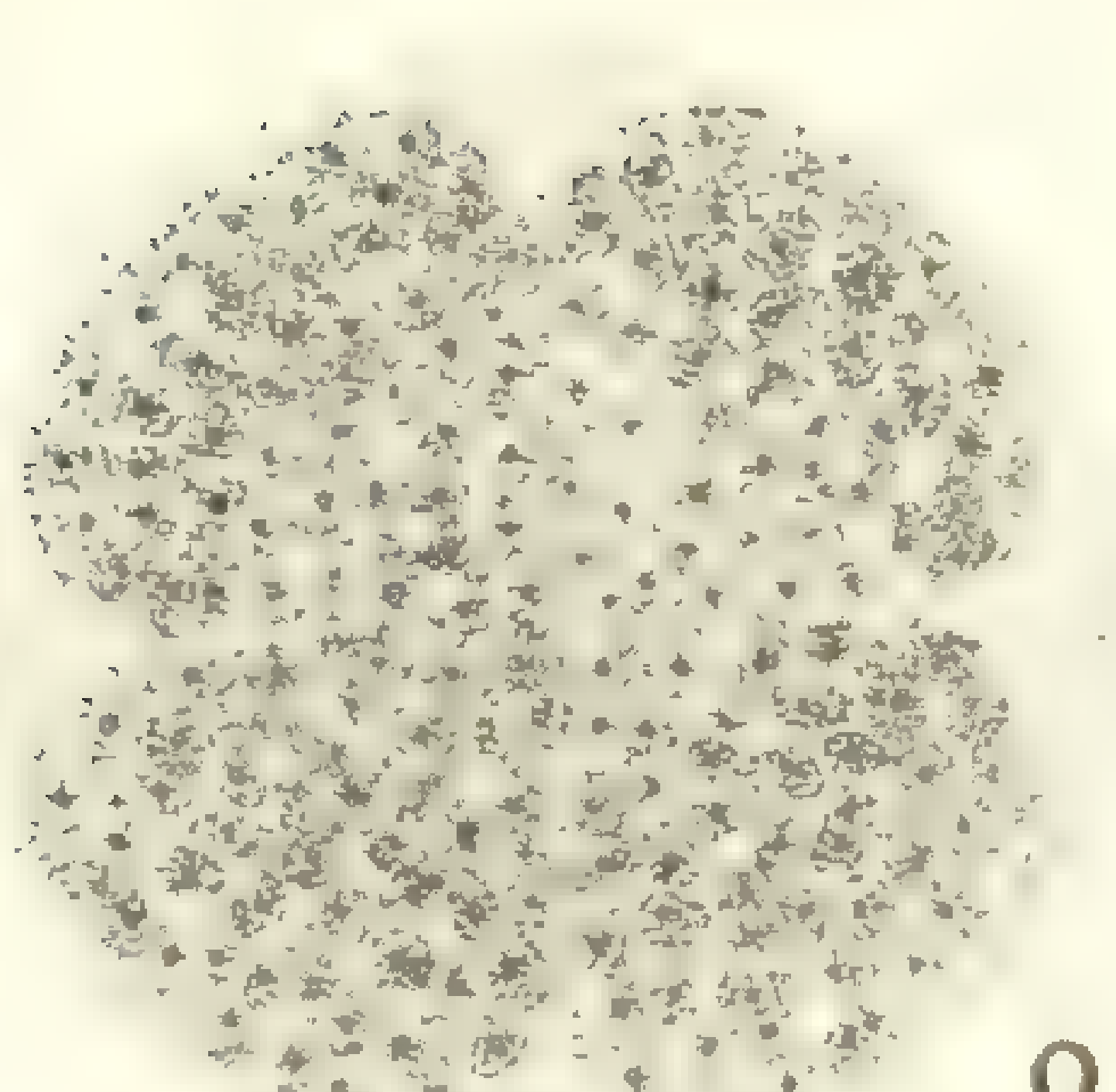

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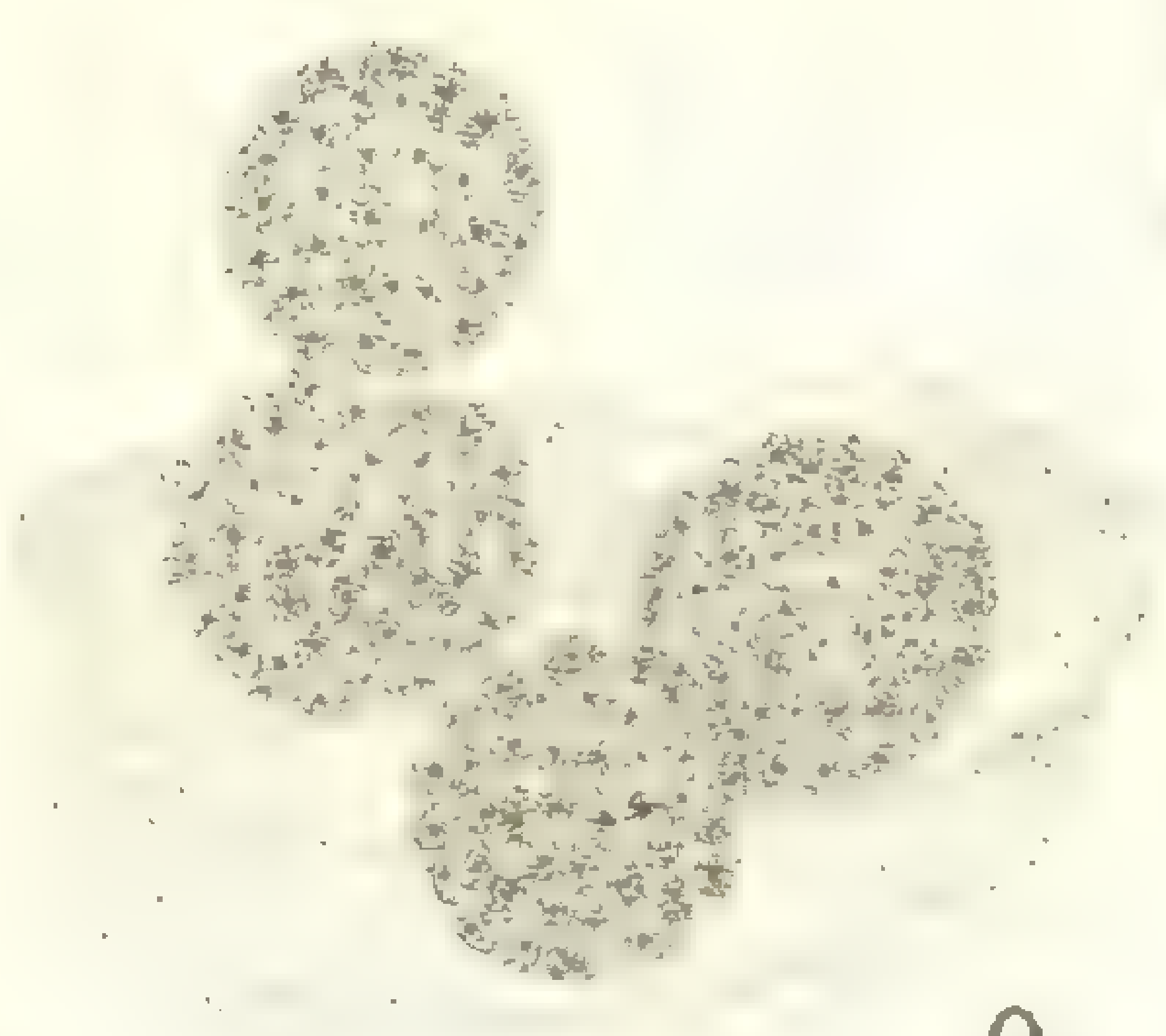

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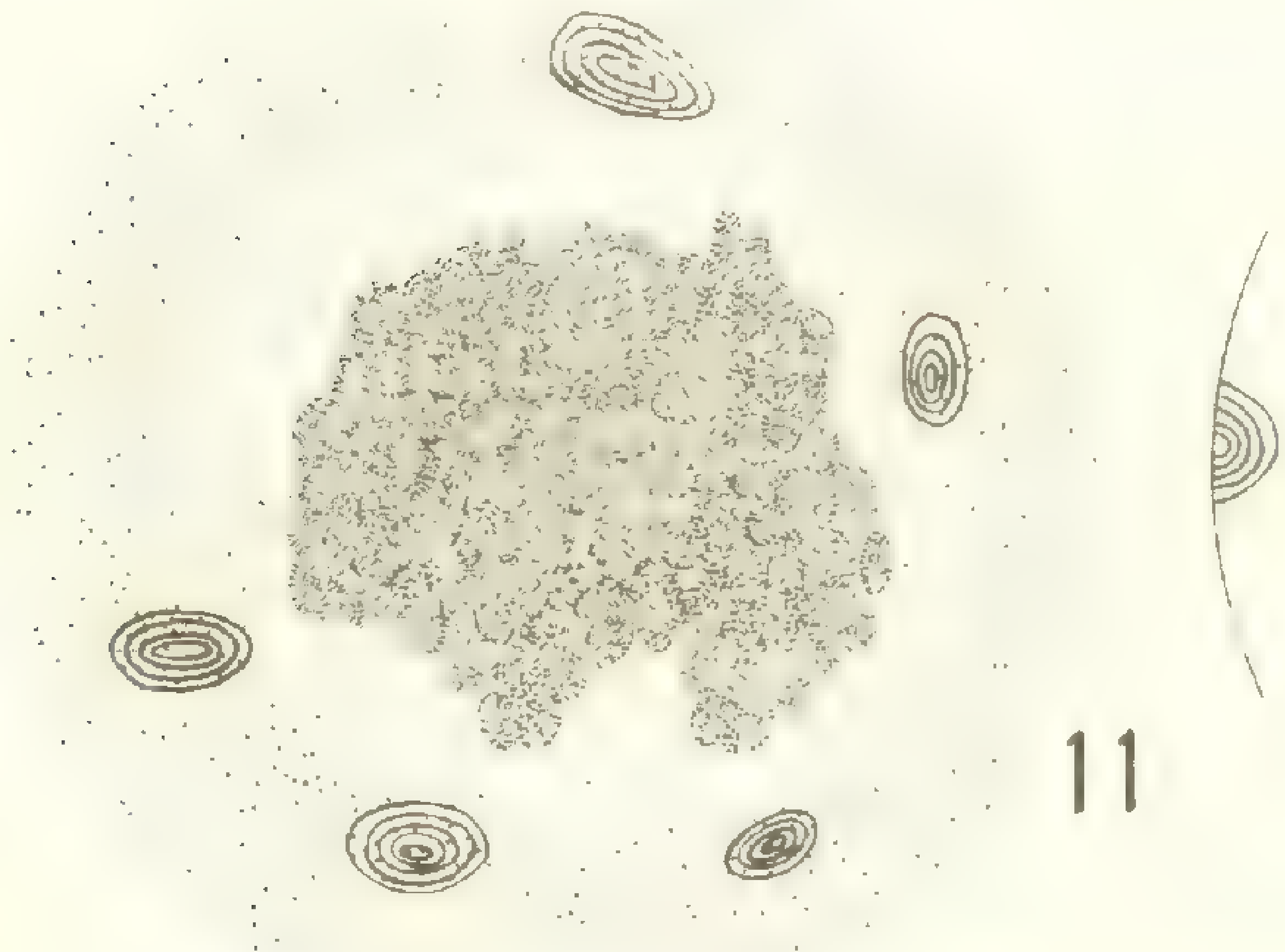
MOORE on EREMOSPHAERA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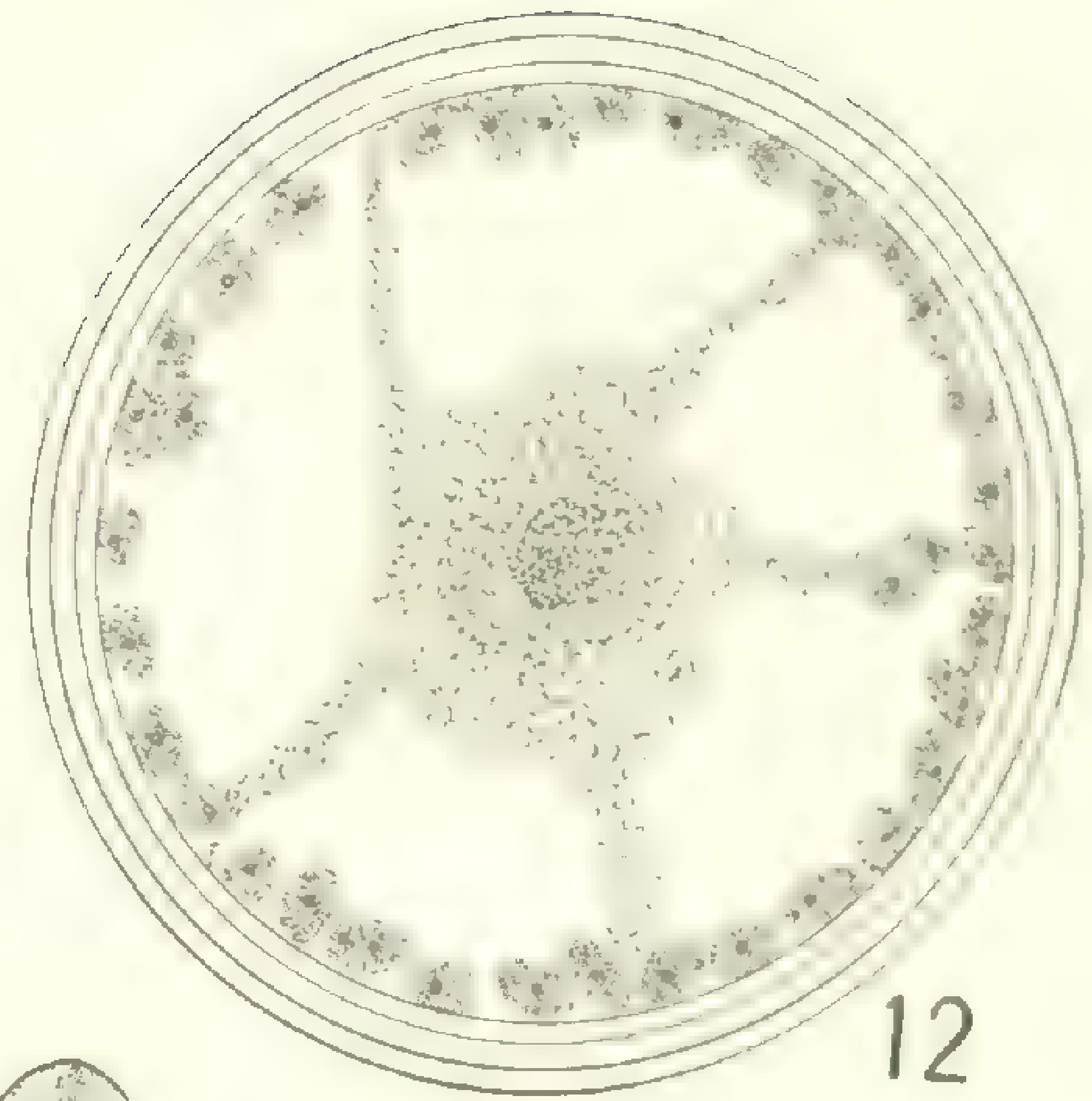
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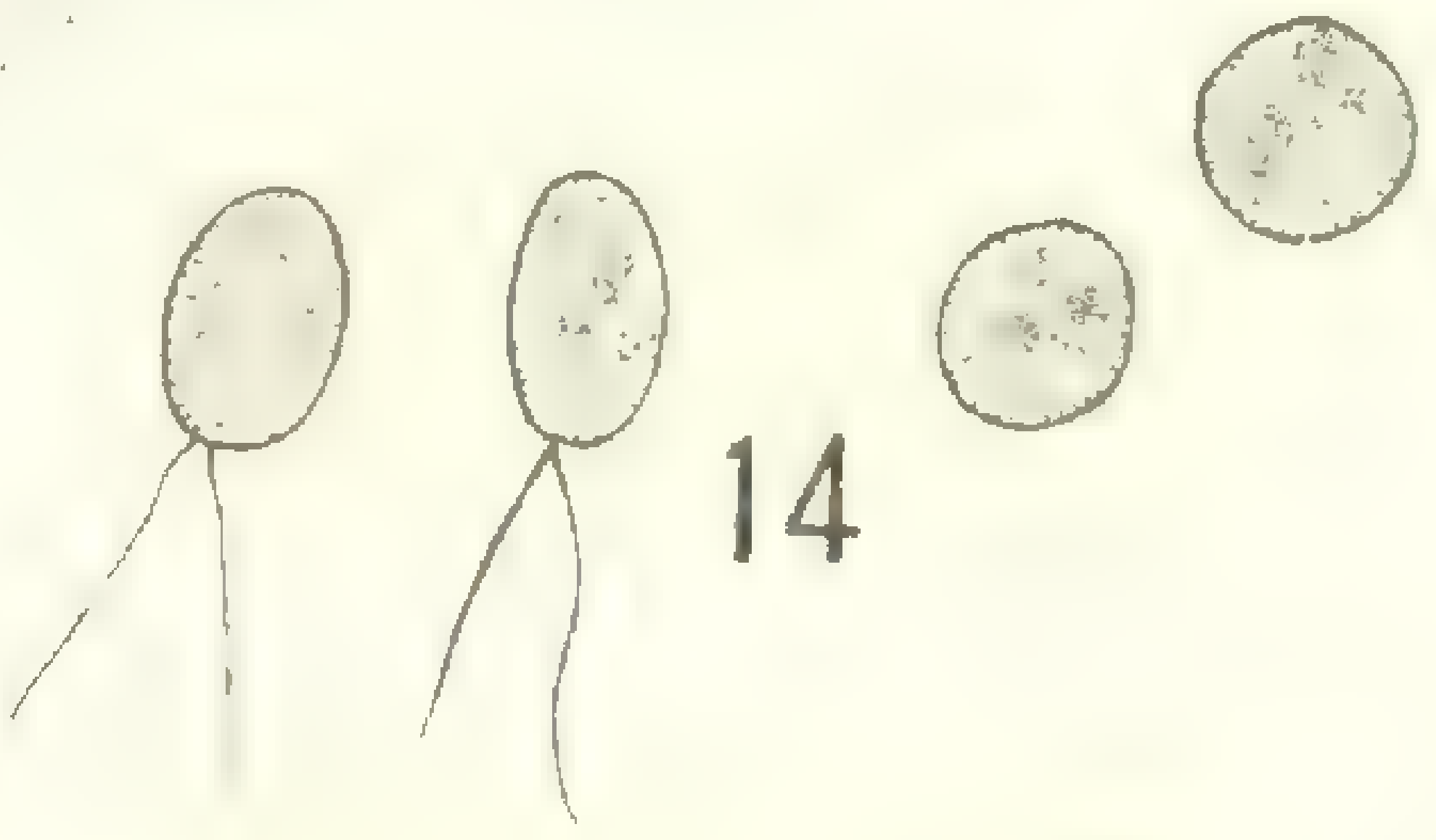
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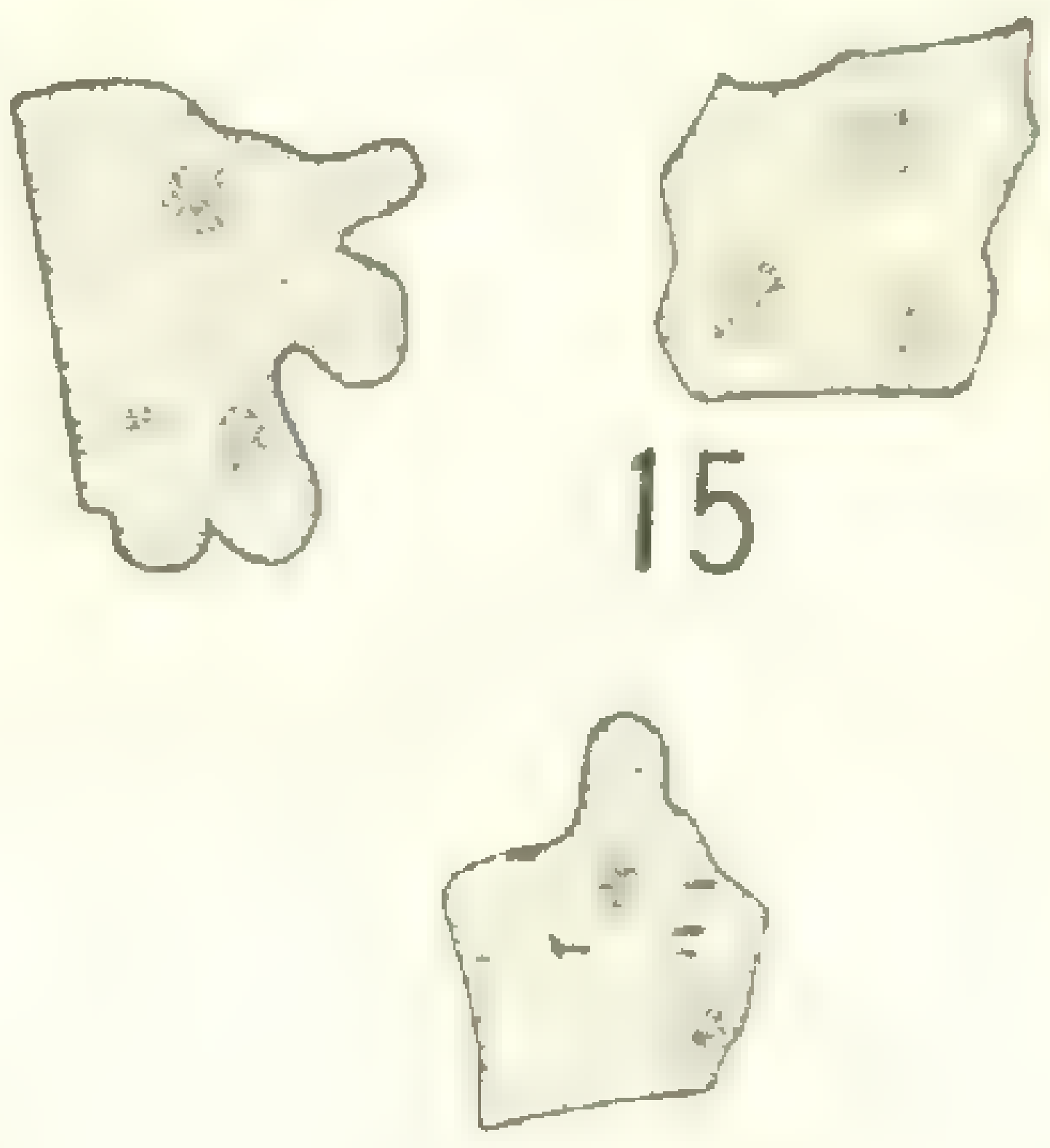
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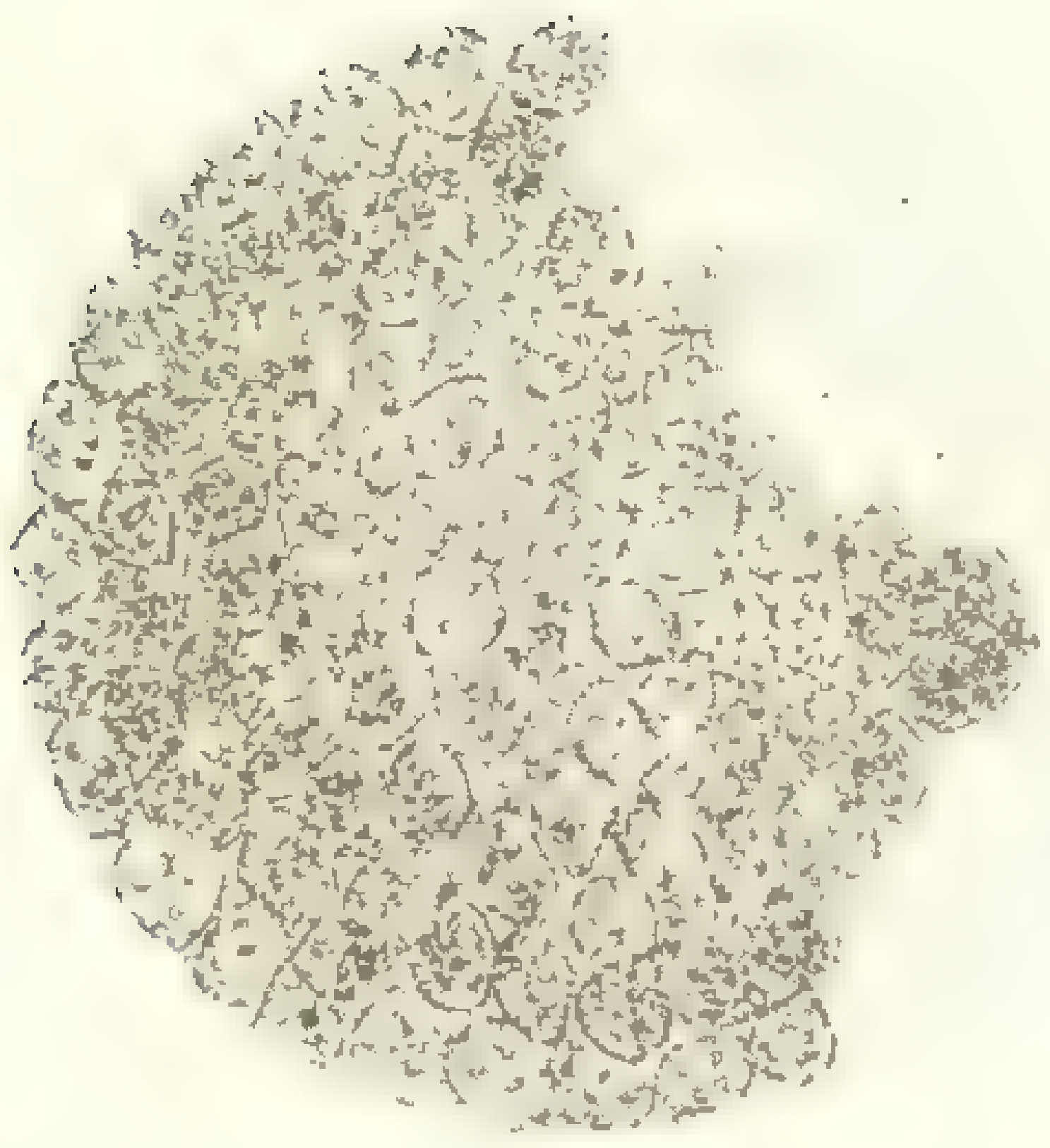
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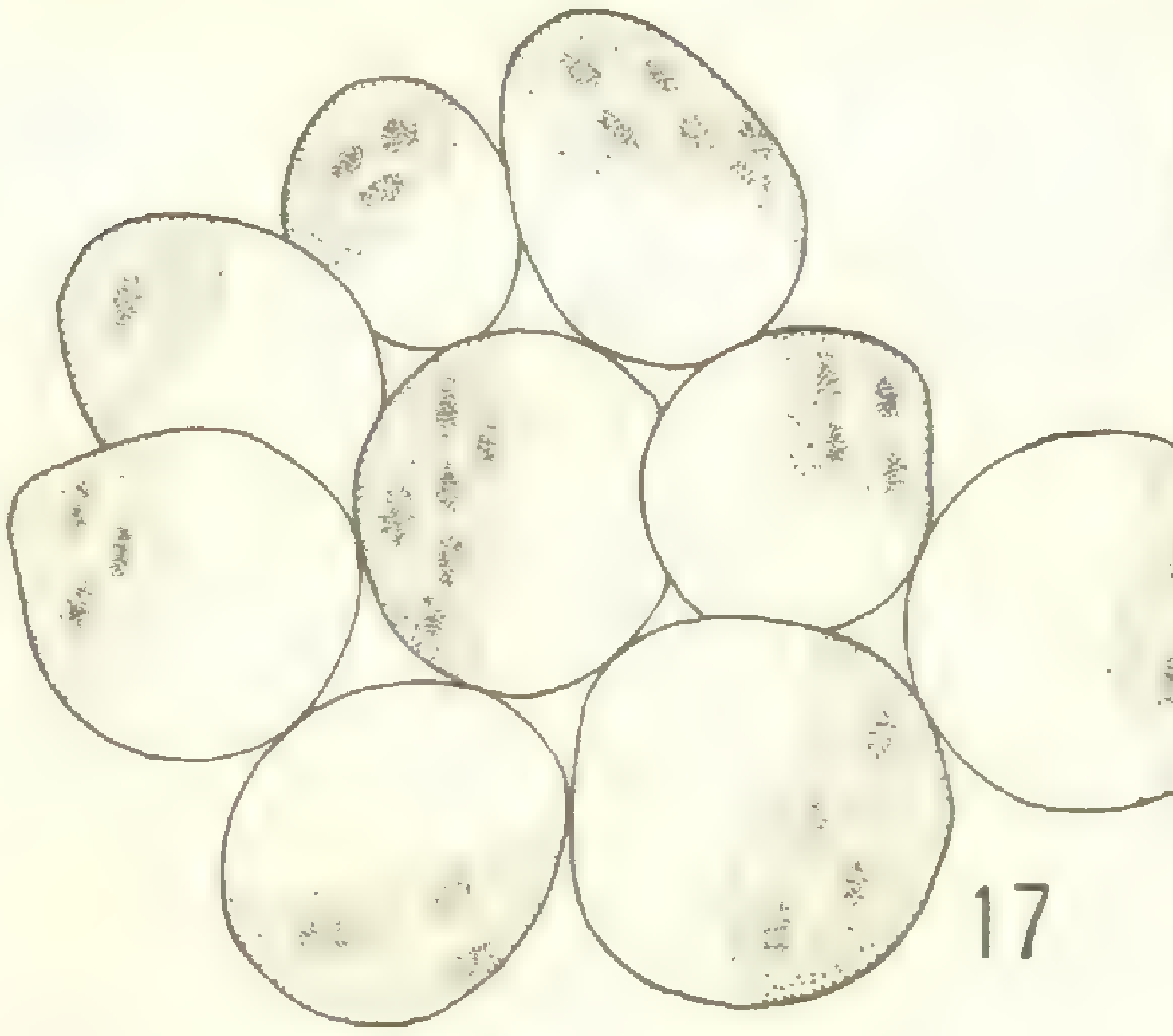
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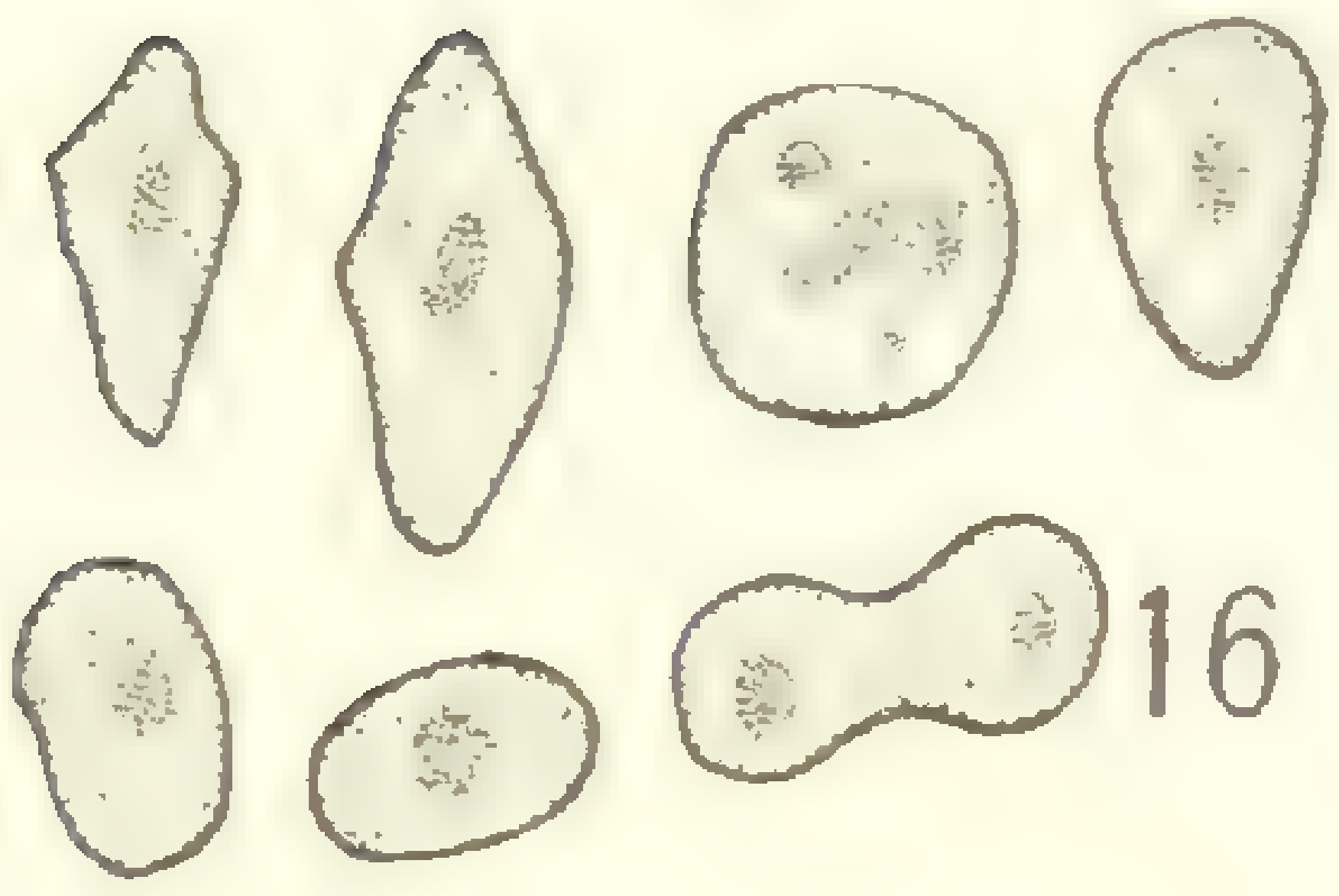
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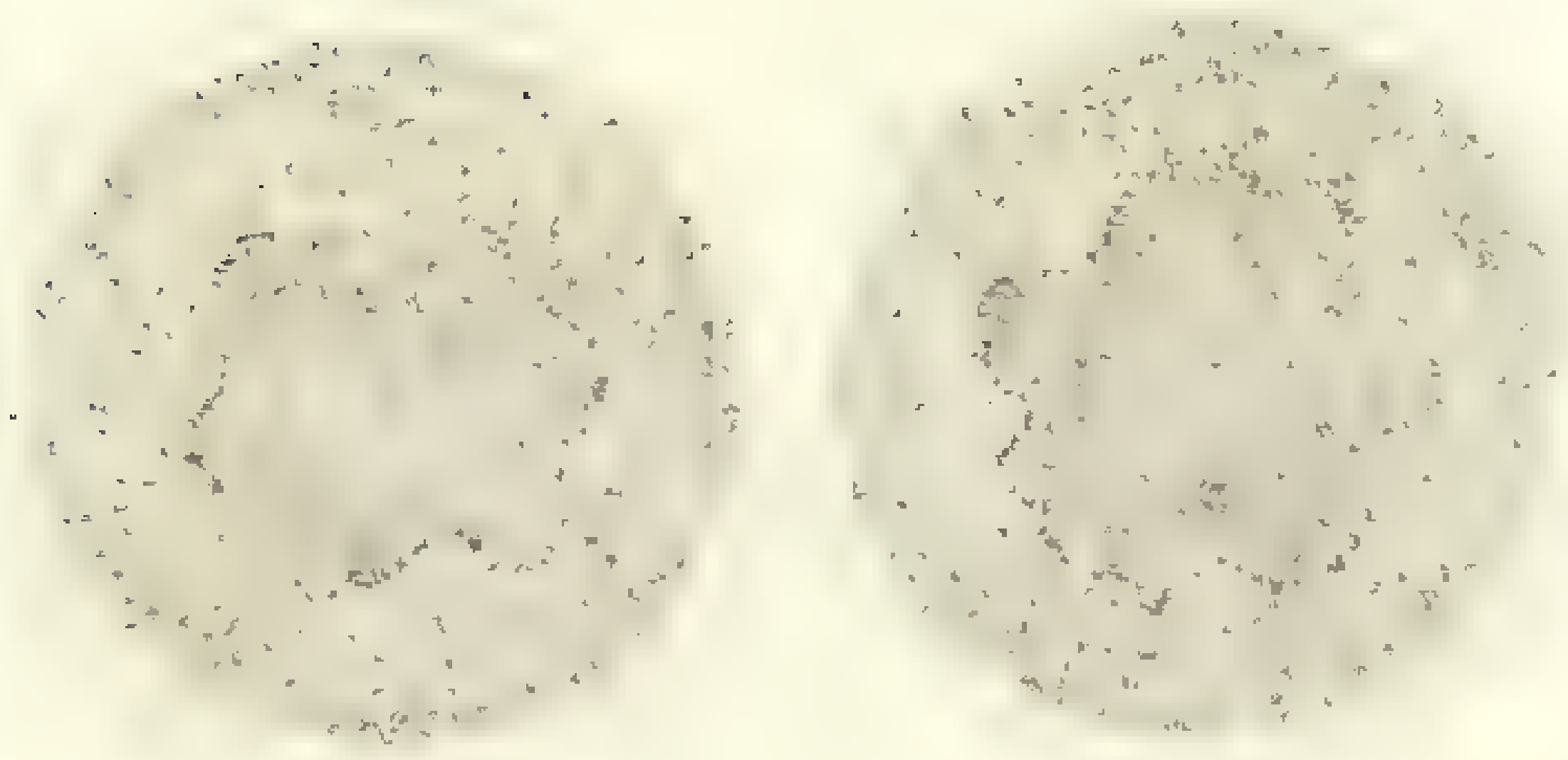
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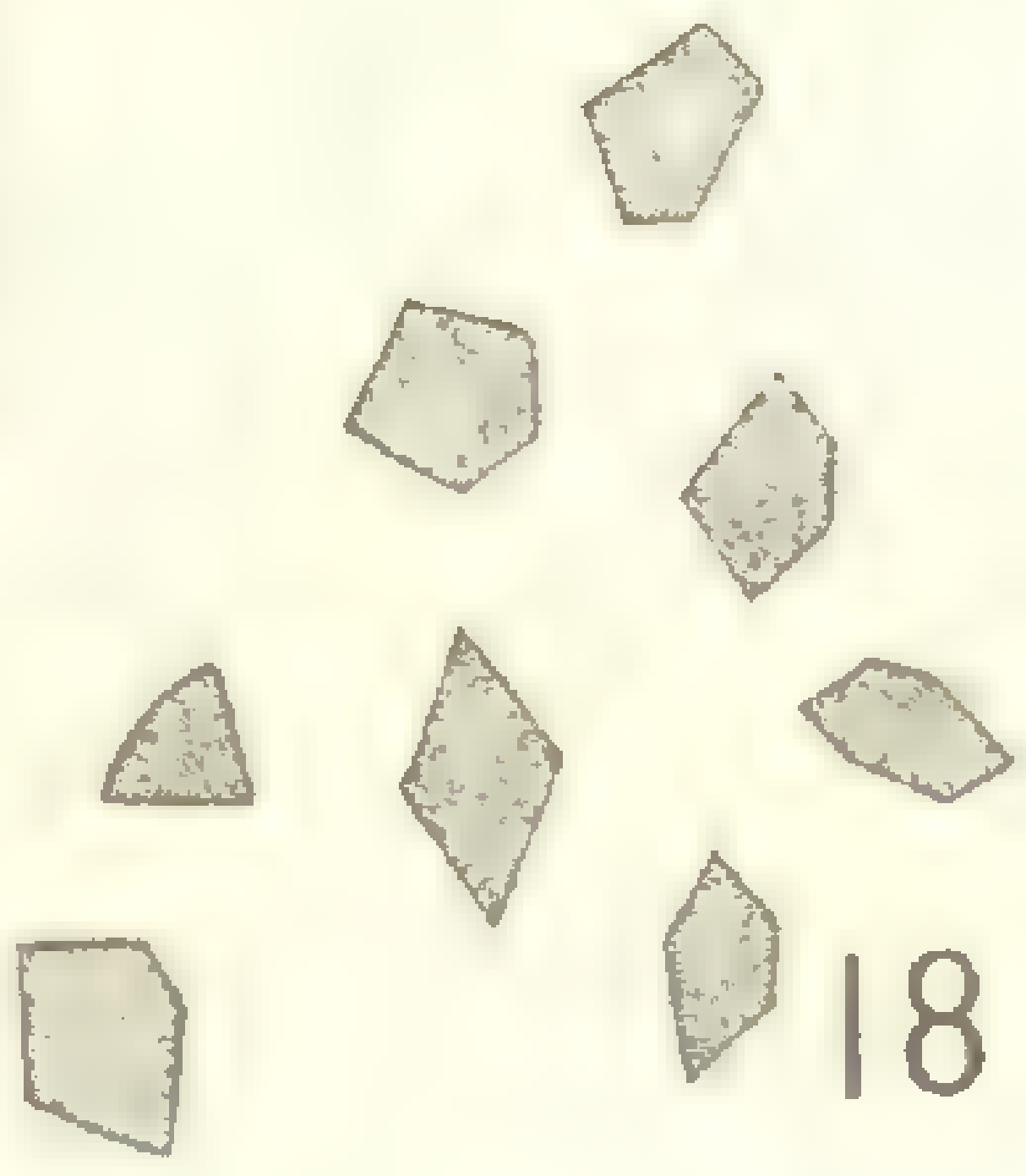
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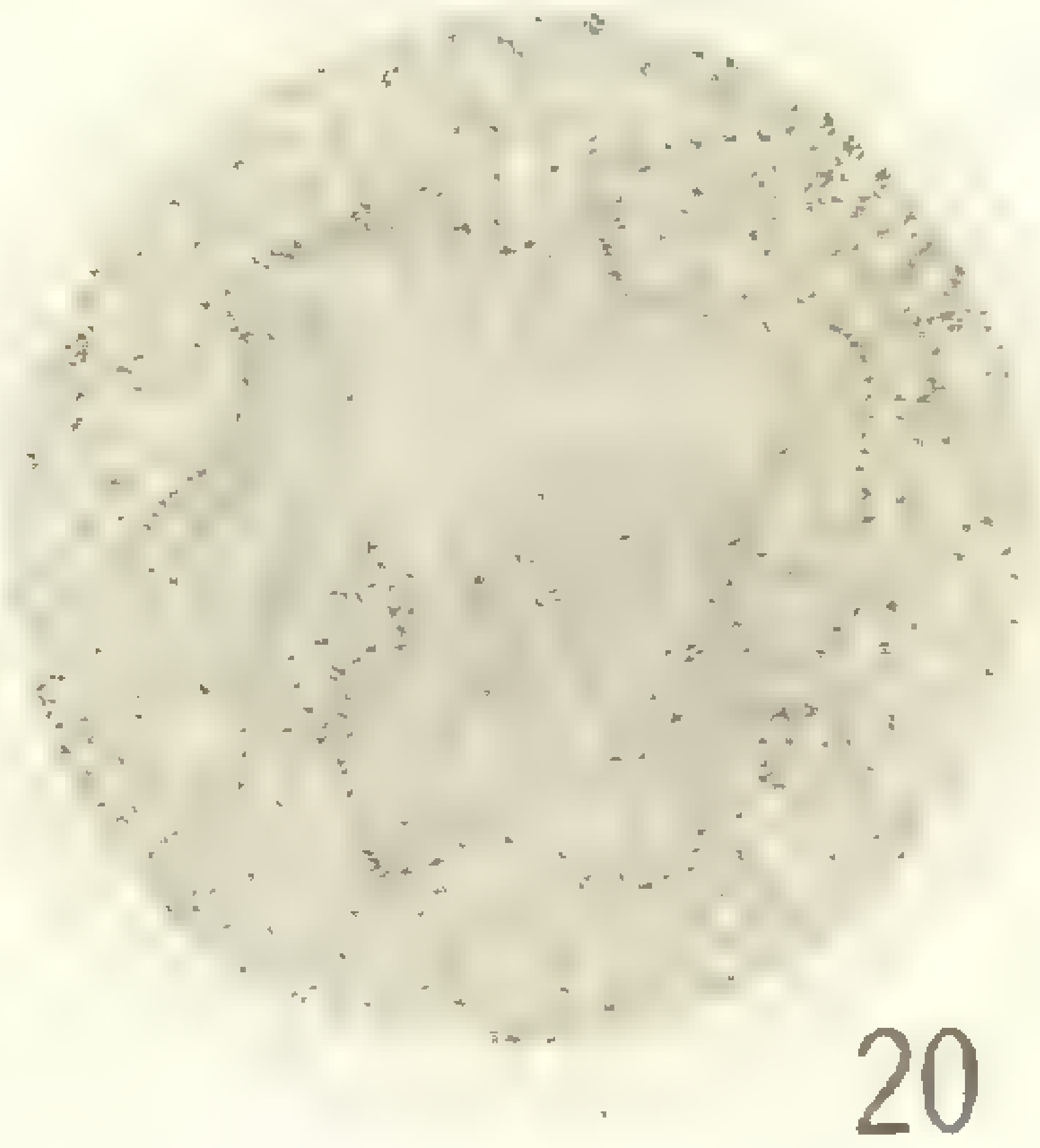
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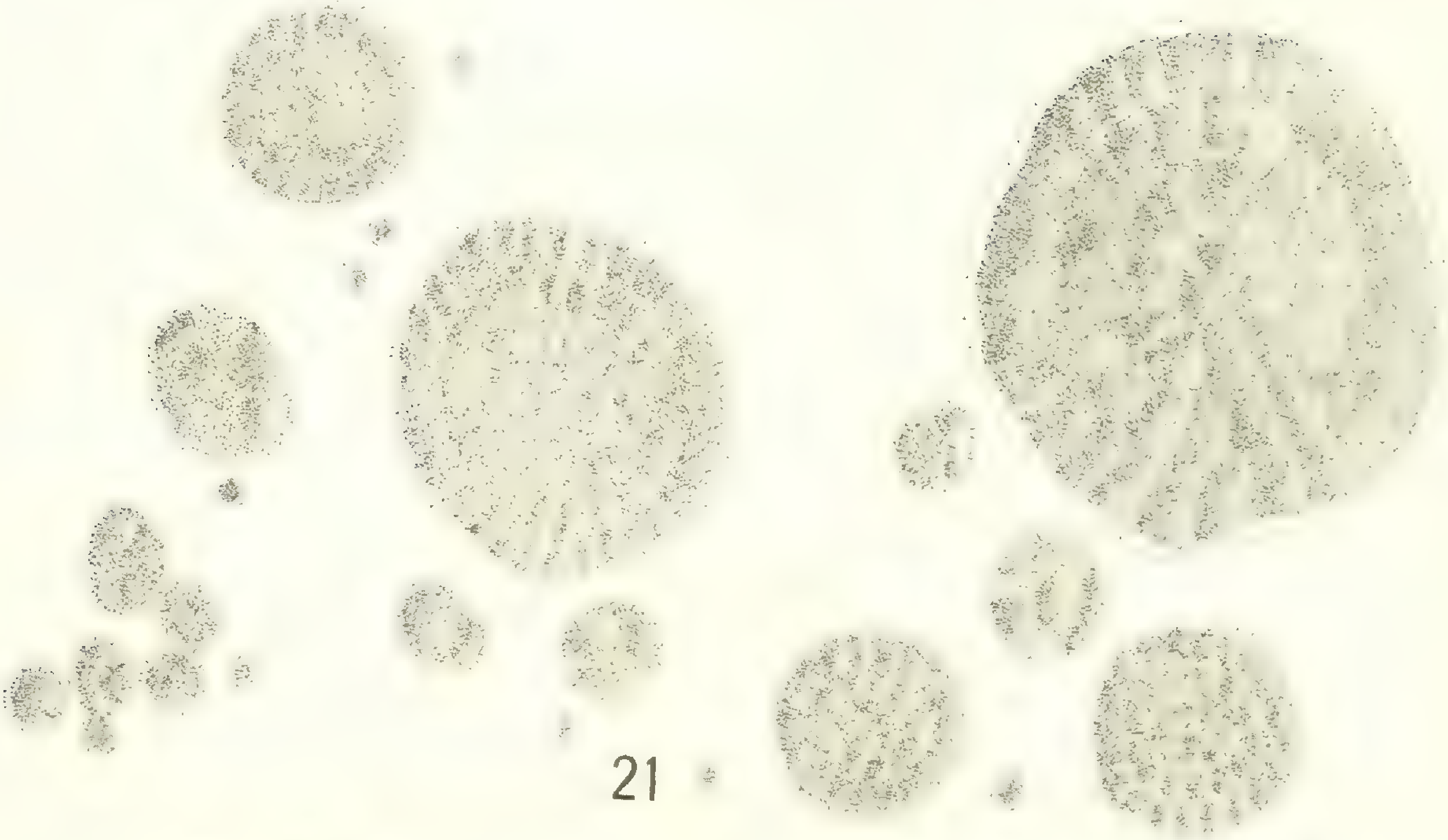
MOORE on EREMOSPHAERA



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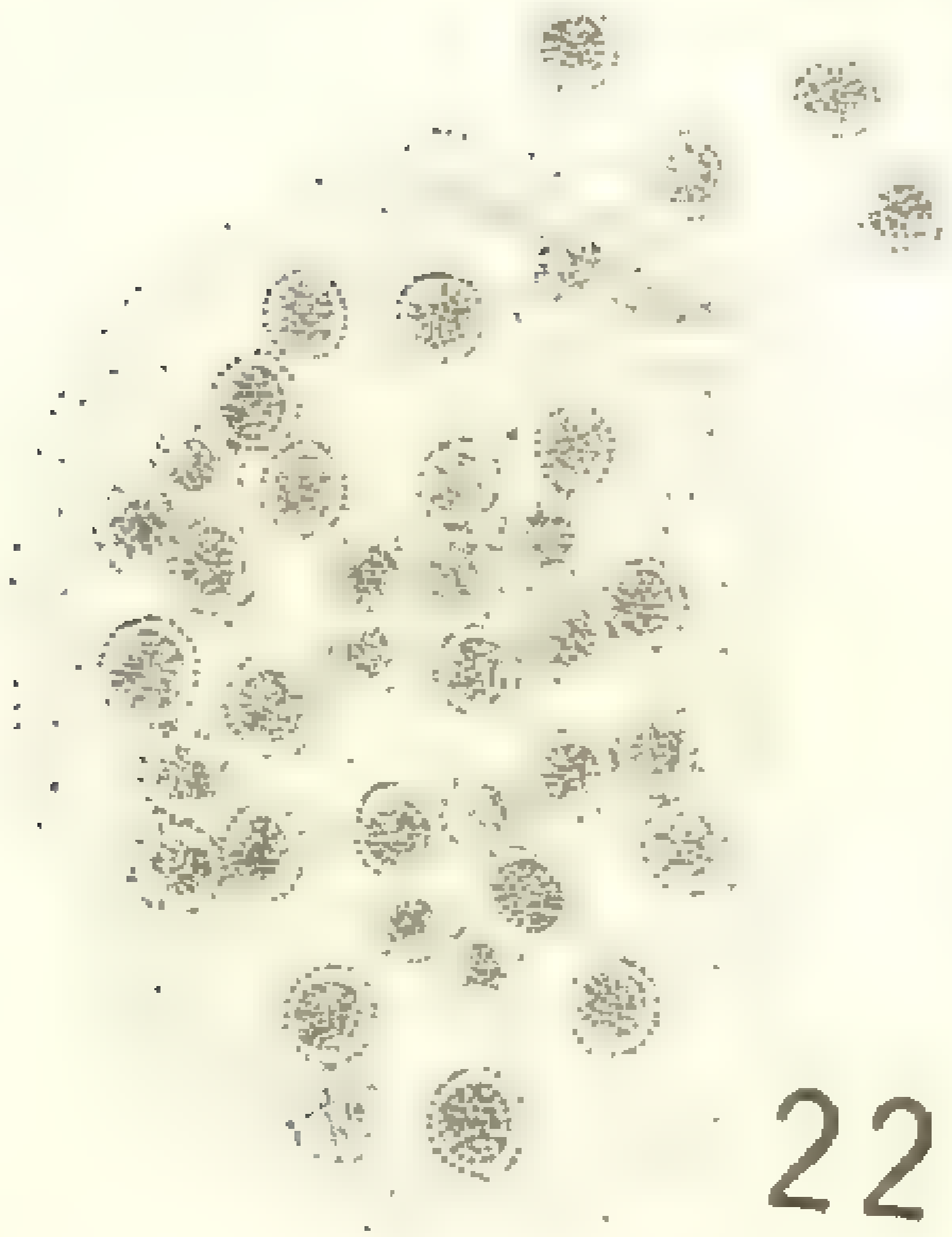

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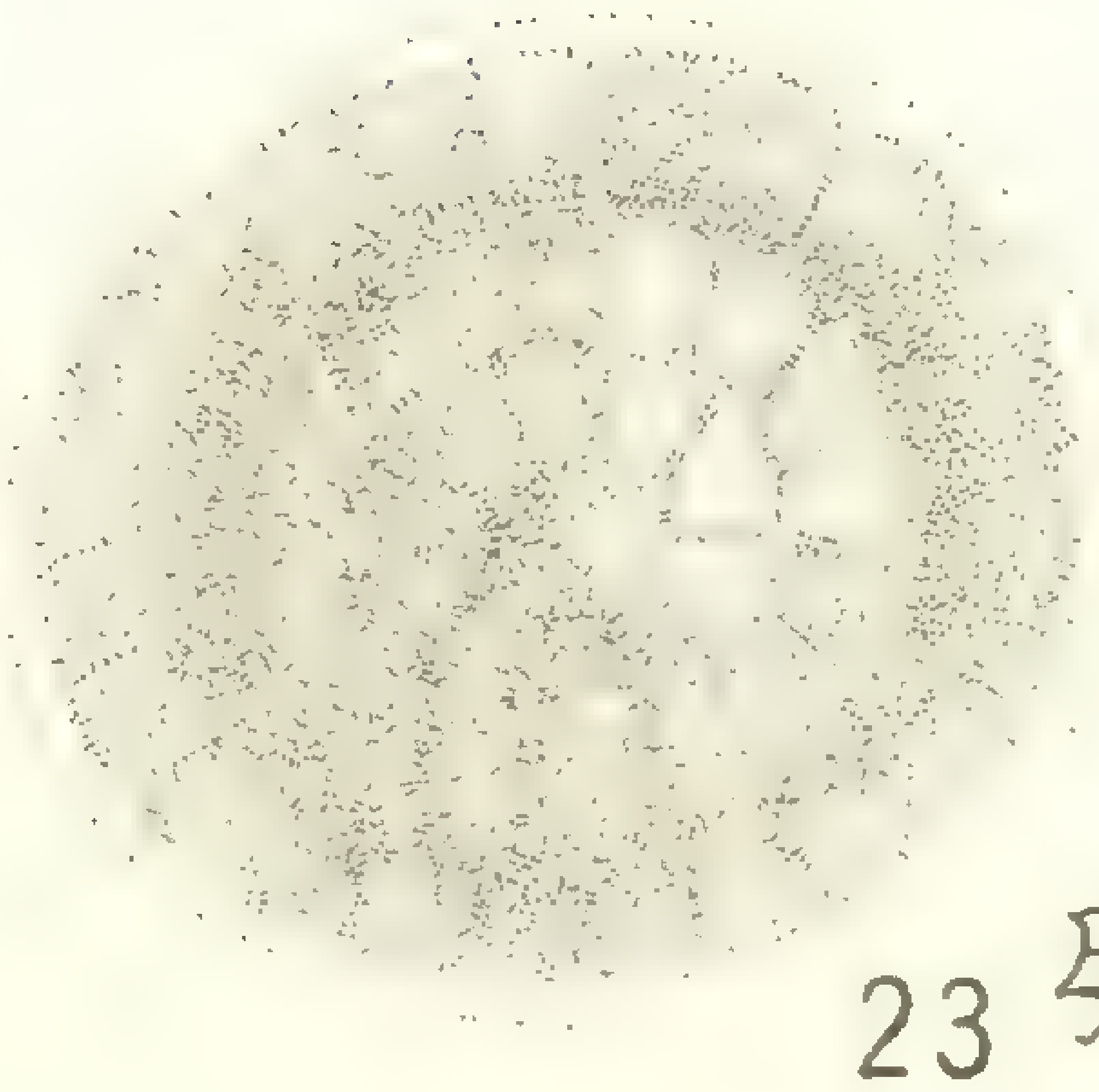

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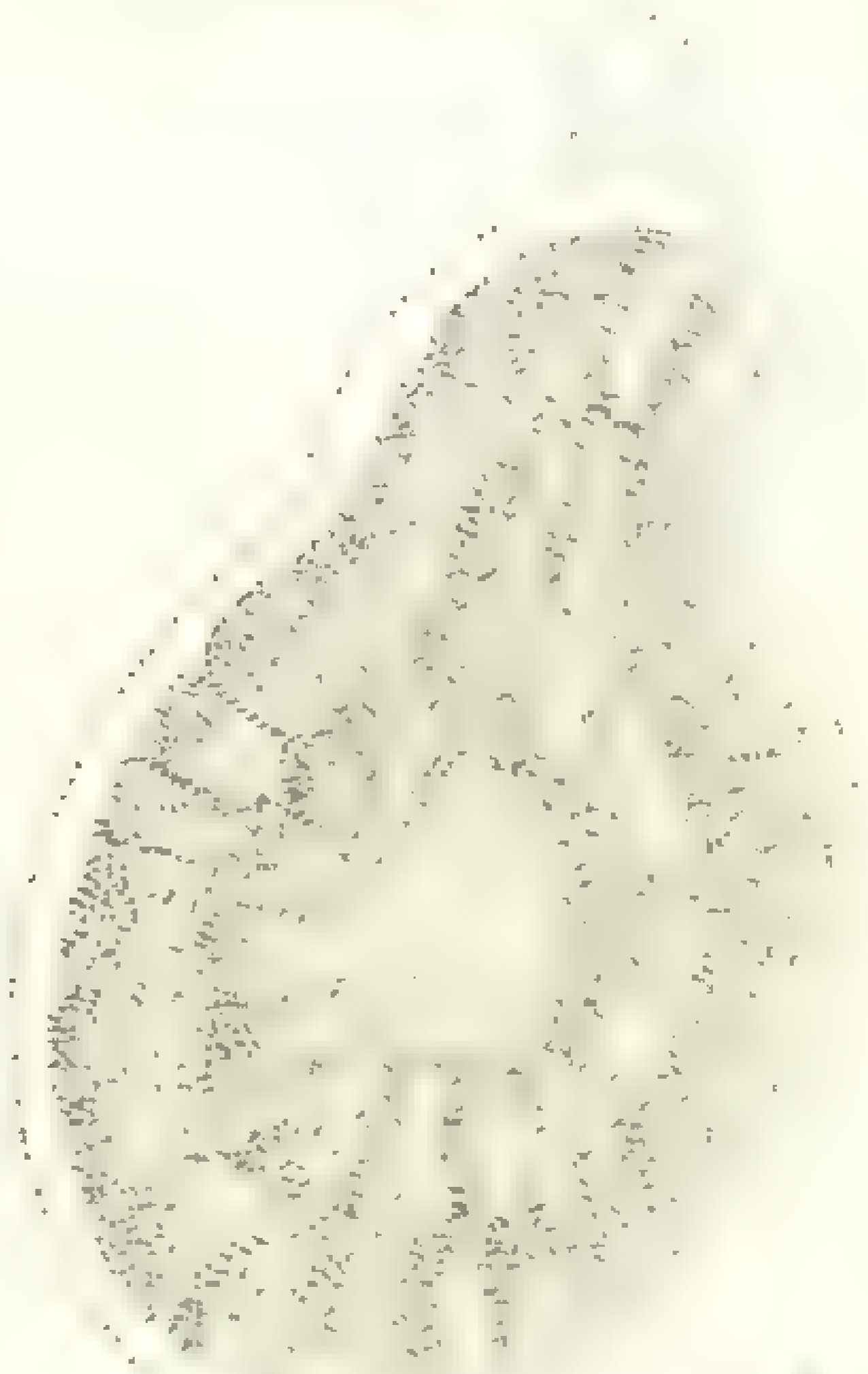

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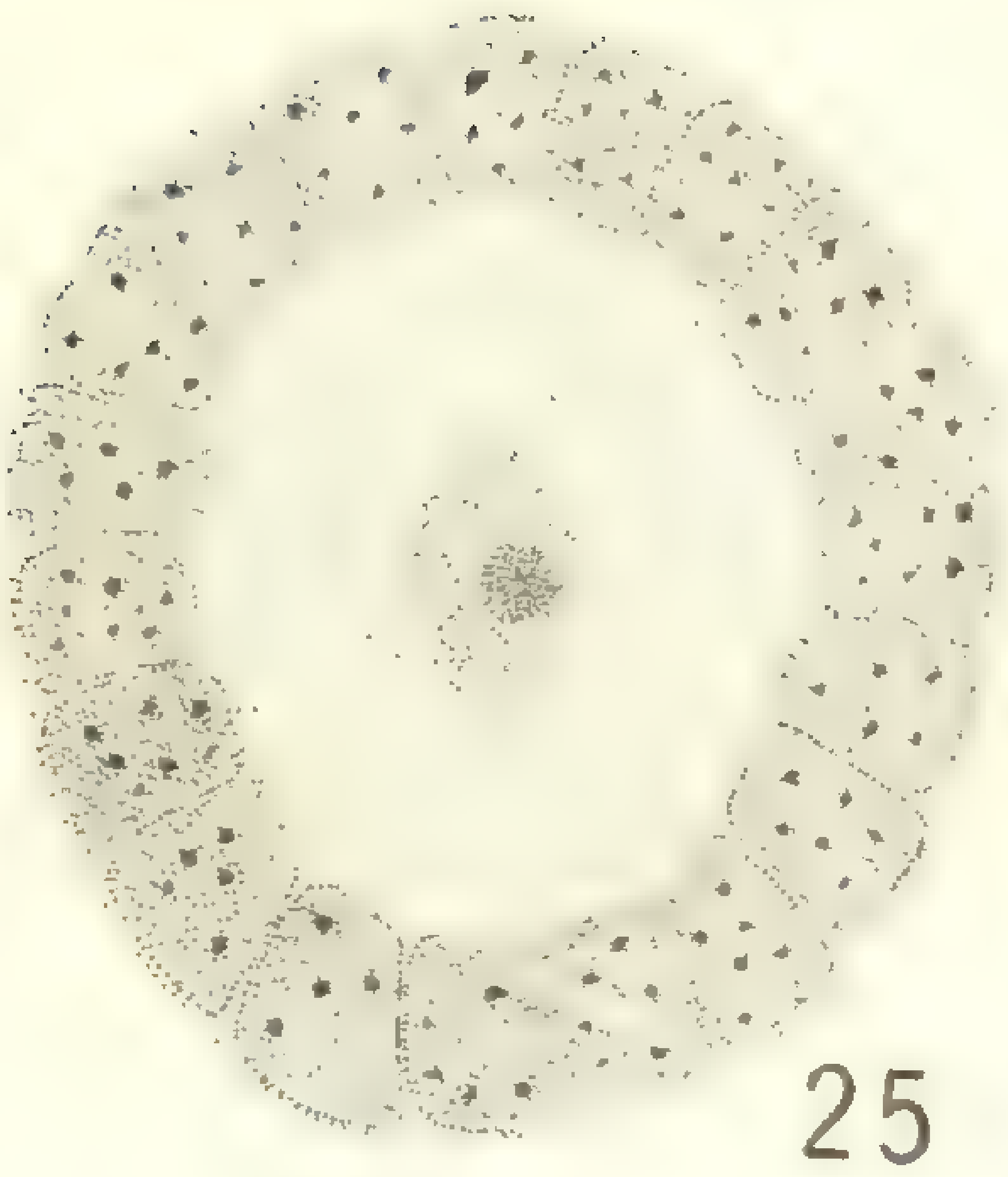

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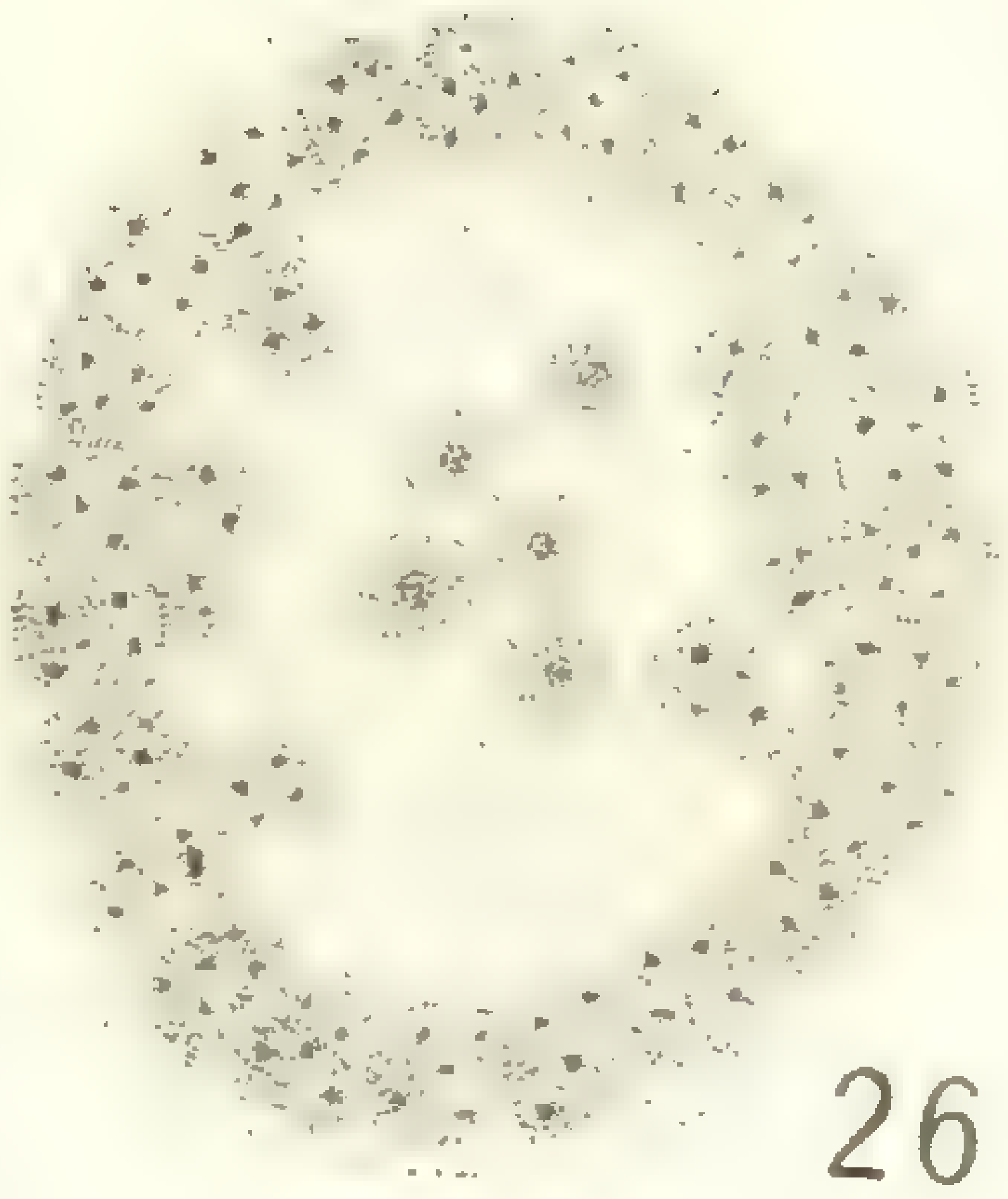

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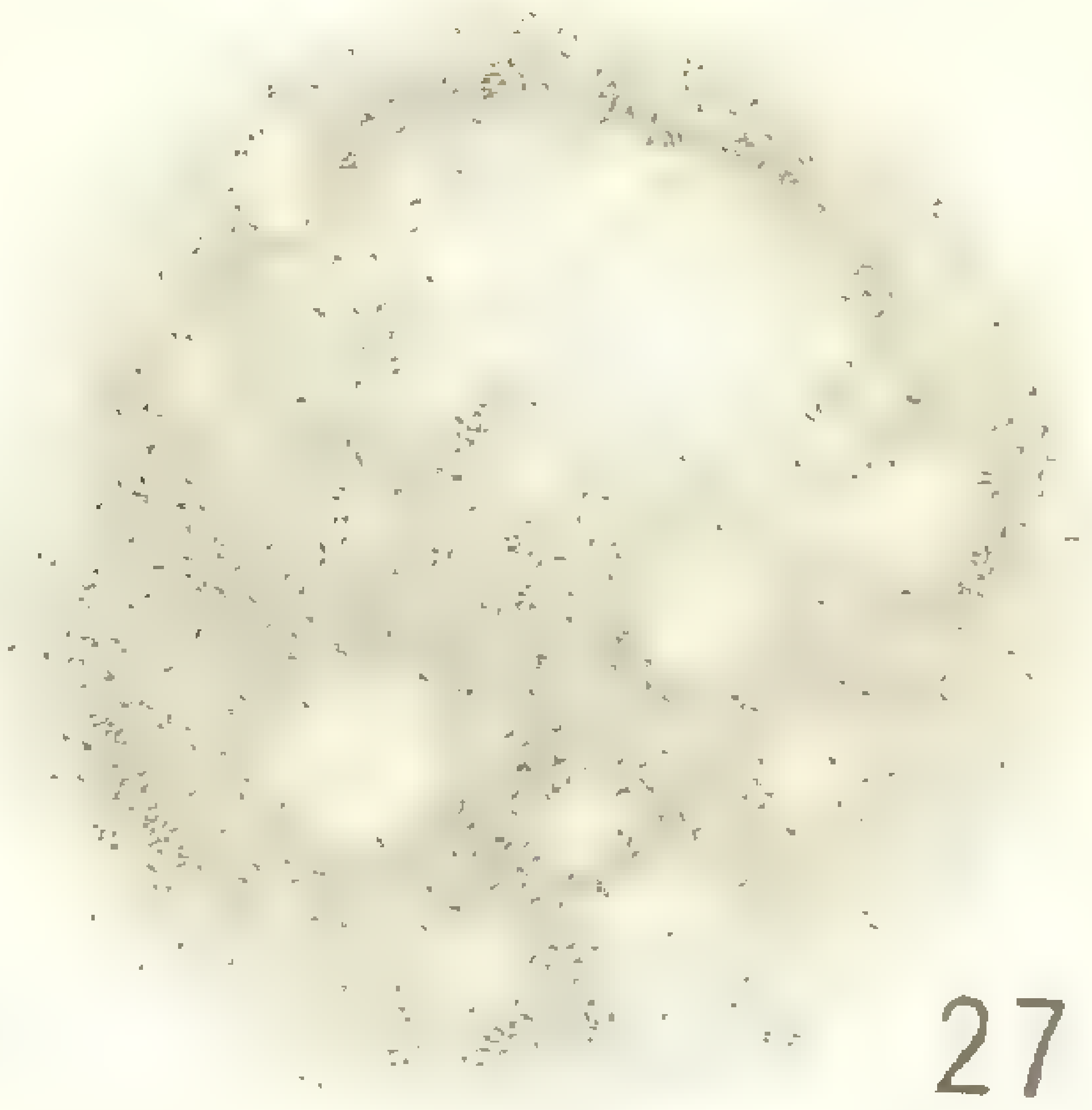

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MOORE on EXCENTROSPHAERA

This work was commenced in the Cryptogamic Laboratory of Harvard University, and my sincere thanks are due to Dr. Farlow and to Dr. Thaxter for their helpful criticism of the investigation carried on while there.

Dartmouth College,
Hanover, N. H.

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5. Henfrey, A., On Chlorosphaera. Trans. Micr. Soc. Lond. 7 : 25–29. 1859.

6. Hofmeister, W. F. B., Ueber die Fortpflanzung der Desmidieen und Diatomeen. Leipzig. 1857.

7. Wille, N., Die natürlichen Pflanzenfamilien, Algen 1^1 : 58. 1897.

8. Wolle, F., Freshwater algae of the United States. 1 : 201. 1887.

EXPLANATION OF PLATES.

All the figures are from ink drawings sketched in with an Abbé camera. In the reproduction they are reduced about one fourth. *Figures 14–18* are drawn with a Leitz $\frac{1}{12}$ (oil), oc. 3; all the others with a Leitz $\frac{1}{6}$ oc. 3. The magnifications given are the original ones before reduction and allow for projection.

PLATE X. Eremosphaera viridis De Bary.

Fig. 1. Surface view of large variety (Ridge hill material). × 250.

Fig. 2. Section of same showing nucleus and protoplasmic strands. × 250.

Fig. 3. Surface view of small variety (Naushon material). × 250.

Fig. 4. Surface view showing the retreat of the chromatophores under the influence of strong sunlight. × 250.

Fig. 5. So-called "rejuvenescence." × 250.

Fig. 6. Beginning of the division into two. × 250.

Fig. 7. Division completed and liberation of daughter cells. × 250.

Fig. 8. Division of mother cell into four. × 250.

Fig. 9. Division completed and liberation of daughter cells. × 250.

Fig. 10. Escape of cell from old wall after "rejuvenescence." × 250.

PLATE XI. Eremosphaera viridis De Bary.

FIG. 11. Surface view and section of wartlike formations in wall. × 250.

FIG. 12. Section showing successive formation of walls. × 250.

FIG. 13. Abnormal condition resembling zoosporangium. × 250.

FIG. 14. Foreign organisms found within cell similar to *fig. 13*. × 830.

FIG. 15. Ultimate development of ciliated organisms. × 830.

FIG. 16. Normal appearance of chromatophores, with pyrenoids. ×830.

FIG. 17. Chromatophores after being crushed out in water. × 830.

FIG. 18. Pyrenoids after treating with chloral hydrate. × 830.

FIG. 19. Resting spores formed immediately after division. × 250.

FIG. 20. Resting spore formed from mature plant. × 250.

PLATE XII. Excentrosphaera viridis Moore.

FIG. 21. General appearance with successive stages in development from spore. × 250.

FIG. 22. Escape of spores. × 250.

FIGS. 23, 24. Cellulose projections of wall. × 250.

FIG. 25. Section through cell, stained to show pyrenoids. × 250.

FIG. 26. Section showing first divisions of nucleus previous to spore formation. × 250.

FIG. 27. Homogeneous appearance of cell previous to spore formation. × 250.

DEVELOPMENT OF THE POLLEN IN SOME ASCLEPIADACEAE.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXII.

T. C. FRYE.

(WITH PLATE XIII)

It is well known that in the Cynanchoideae[1] the microspores of each sporangium adhere in a mass, forming what is known as a pollinium. This is true also of some of the Orchidaceae and Leguminosae. Since the three families mentioned are all highly specialized for insect pollination, the adherence of pollen may perhaps be regarded as having no special morphological significance. The Asclepiadaceae are further exceptional in the production of only two sporangia in each stamen. In the Balanophoraceae, Orchidaceae, and Mimosoideae, the number of microsporangia is variable. The large number in some of the Mimosoideae is attributed to the interjection of plates of sterile tissue. In the same way *Lemna minor* is said to form four, the normal number, from a single mass of archesporial tissue.[2] The question arises whether, in the Cynanchoideae, there is any indication of suppression or fusion of sporangia in the earliest stages of their development. More interesting does this become when we recall that in the small group Secamoneae the pollinium in each half anther is paired, but the parts adhere closely.

Little is known about the formation of pollen in the Asclepiadaceae. In the Periplocoideae tetrads are formed, the microspores adhering in groups of four when mature. Of the pollen development in the Cynanchoideae almost nothing is known.

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[1] The author follows the classification of Engler and Prantl in *Die natürlichen Pflanzenfamilien*.

[2] CALDWELL, O. W., On the life history of *Lemna minor*. BOT. GAZ. **27**: 37–66. 1899.

Chauveaud[3] claims that the pollen mother cells of Cynanchum divide, but mentions only one division, with reduced number of chromosomes, the pollen grains forming from the daughter cells. Here one is left to infer that a mother cell formed only two microspores, or that there was a second division which escaped his observation. Wille[4] examined *Asclepias speciosa*, but was unable to find tetrads. Strasburger[5] finds no tetrad division in *Asclepias Syriaca*. He finds in the anthers what he terms sporogenous cells, radially elongated, large, and rich in contents. These divide by cross walls into two, and the longest, near the middle of the sporangium, into four. He says the resulting cells are homologous with the pollen mother cells of other plants, and develop into microspores without further division. So far as I have been able to learn Zostera[6] and the Cynanchoideae are the only Angiosperms which are reported to form their pollen without tetrad divisions. It was thought that there were no tetrad divisions in the Cyperaceae until Juel[7] found that the nuclear division occurred, but no walls were formed. The reported different pollen formation in Cynanchum and Asclepias, the presence of tetrads in the Periplocoideae, and the small number of cases of pollen formation without tetrad division, all seem to warrant an investigation of the formation of microspores in the Cynanchoideae.

In the spring of 1901 I undertook the task of looking into the pollen formation of some members of the Asclepiadaceae growing abundantly in the vicinity of Chicago. Those examined were *Asclepias Cornuti*, *A. tuberosa*, *A. phytolaccoides*, *A. incarnata*, *A. verticillata*, *Acerates viridiflora*, and *A. longifolia*.

In *A. Cornuti* I was able to trace the development from the archesporium to the pollen mother cell. The first indication of the formation of sporangia is the increase in length of the hypodermal cells on the inner side of the stamen on each side of its median line, thus forming the archesporium (*fig. 1*). While both sporangia are formed from the same continuous layer, they are separate from their beginning; and there are no indications of four. The tapetum on the dorsal side of the sporangium is formed from the third layer of cells — the one next the archesporium. The archesporial cells elongate at right angles to the inner surface of the stamen and divide transversely, resulting in an inner primary sporogenous, and an outer primary wall layer. The beginning of this division is shown in *fig. 1*. By transverse divisions of the primary wall layer there arise four wall layers (*fig. 3*), the inner one or two of which form the tapetum. The tapetal nature of these cells is already evident in their large nuclei and nucleoli, and their deeply staining contents, before they have completed their division (*fig. 4*). In some places the tapetum is composed of one layer, in others of two. Where there are two the outer is often composed of flattened, the inner of isodiametric cells (*figs. 6* and *14*). While the primary wall layer forms its four layers, the plate of cells dorsal to the sporangium also divides and takes on its tapetal character. The primary sporogenous cells contain large vacuoles, while their nuclei are near the middle (*fig. 4*); but even at this stage of development they grade into ordinary vegetative cells at the outer edge of the sporangium, so that it is difficult to determine just where they cease to be sporogenous cells (*fig. 3*). Enough stages were seen in the other species mentioned to warrant the conclusion that the development of the pollen in them is the same in general as in *A. Cornuti*.

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[3] De la reproduction chez les dompte-venin 41. (Diss.) Paris, 1892.

[4] Ueber die Entwickelungsgeschichte der Pollenkörner der Angiospermen 41. 1886.

[5] Ueber das Wachsthum vegetabilischer Zellhäute. Histologische Beiträge **2** : 80. 1889.

[6] HOFMEISTER, Bot. Zeit. **10**: 121. 1852.

[7] Beiträge zur Kenntniss der Tetradentheilung. III, Die Entwickelung der Pollenkörner bei Carex. Jahrb. f. wiss. Bot. **58** : 649. 1900.

From this point the history was most completely followed in *A. tuberosa*. The primary sporogenous cells become the spore mother cells without further division. This is indicated by the nature of the nuclei and by the form and number of the chromosomes. The size of the nucleus increases, and the chromatin collects in granular tangled threads, which together with the large nucleolus form the staining contents of the large transparent nuclear vacuole—the synapsis stage of the nucleus (*fig. 7*). This stage of the nucleus was also observed in *Asclepias Cornuti*, *A. phytolaccoides*, *A. verticillata*, and *Acerates longifolia*. At the beginning of mitosis the nucleolus often separates into several smaller nucleoli. The chromatin in *A. tuberosa* breaks into five chromosomes which split longitudinally while scattered in the nuclear vacuole (*fig. 6*). They are very small when split, but become much larger as the nuclear wall and the nucleoli disappear (*fig. 6*). After the disappearance of the nucleoli they are short, thick, and much larger than those in the vegetative cells. The number of chromosomes in the spore mother cells is approximately half that in the vegetative cells (compare *fig. 6* with *figs. 8* and *9*). The exact number in the vegetative cells I was unable to determine. This reduction of chromosomes occurs in the spore mother cells of other plants. The mitotic phenomena attending the division of the cells referred to as spore mother cells closely agree, then, with those in the spore mother cells of other plants, and do not agree with those in the vegetative cells. This is to me conclusive evidence of their spore mother cell nature.

Closely following this division, often before the cross wall is distinguishable, comes the second, with smaller chromosomes, which results in a row of four daughter cells representing a tetrad (*fig. 10*).

Both the rapid succession of these divisions and the formation of four and only four cells from a mother cell homologize well with tetrad formation. Each mother cell divides; those at the pointed upper end of the sporangium slope outward and downward, as shown in *fig. 5*, thus permitting the division of all the cells without great difference in size. The lower end of the sporangium is rounded, and hence the cells there are not greatly modified. These divisions I have no doubt are the ones Strasburger saw in *A. Syriaca*, and this creates a doubt in my mind whether the mother cells near the ends of the sporangia formed only two microspores, as the report would lead one to believe.

This formation of microspores in a row, while not the usual tetrad form, is not peculiar to the Asclepiadaceae. The cells are reported in other arrangements in *Typha latifolia*,[8] *Orchis mascula*,[9] Juncus,[10] and some members of the Periplocoideae.[11]

The cells now become isodiametric, irregular, and crowded. Adjusting themselves to each other they soon lose all indication of their origin as a row of four. The protoplasm becomes filled with short coarse threads which stain readily and obscure the other cytoplasmic structures (*fig. 11*). The walls then thicken very rapidly. This is by the deposition of a layer from within the cells, as is evident later when intercellular spaces appear. When a mature pollinium is cut and squeezed the walls separating the microspores split, and the microspores are squeezed out whole. Where a microspore is in contact with a pollinium wall it separates from it an inner layer (*fig. 16, x*). This suggests that most of the pollinium wall is of a different origin from the walls of the microspores. The nucleus divides after the walls are thickened, forming the generative and tube nuclei (*fig. 13*). The tube nucleus is much the larger and denser. The generative nucleus moves to the side of the cell (*fig. 14*), and is cut off by a wall of considerable thickness (*fig. 15*). The tapetum gradually disintegrates, leaving the pollinium loose in the anther, except for its attachment to the caudicle by its upper end. After the walls begin to thicken the thready protoplasm collects in masses within the cells (*fig. 12*). The masses disappear about the time of the formation of the generative and tube nuclei, and dense fusiform bodies composed of one or more strands, and of unknown nature, make their appearance. In *A. verticillata* they were short, thick, and smaller than in the other species. Their origin may be connected with the thready and dense protoplasm just preceding their appearance. They remained and were seen even in the pollen tubes. The pollen of all the species studied contained them, but they were most abundant in *A. Cornuti*. The tests for calcium oxalate, carbonate, phosphate, and sulfate, and for silicon and starch failed to reveal their nature. They stain like chromatin.

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[8] Schaffner, J. H., Development of the stamens and carpels of *Typha latifolia*. Bot. Gaz. **24**: 93. 1897.

[9] Wille, Ueber die Entwickelungsgeschichte der Pollenkörner der Angiospermen 39. 1886.

[10] *Ibid.* 42.

[11] Schumann, Engler and Prantl, Nat. Pflanzenfam. 4^2: 196. 1895.

A stage like that in *fig. 16* was frequently found, and seems to indicate the fragmentation of the tube nucleus, although the series about it was not close enough to justify a definite conclusion.

Germination always bursts the pollinium along its outer edge, at the point where the diameter is greatest (*fig. 17*). A cross section shows the pollinium wall to be thinnest there. Germination of the microspores was observed in *A. Cornuti*, *A. tuberosa*, and *A. incarnata*.

SUMMARY.

The development of the sporangia in the Asclepiadaceae studied is the same in general as in other plants, while there are no indications of the phylogenetic history of the reduction in number. The primary sporogenous cells without further division become the pollen mother cells. The latter divide each into four with the usual phenomena accompanying tetrad division, but through mutual adjustment and the close adherence of the microspores the evidences of grouping are lost.

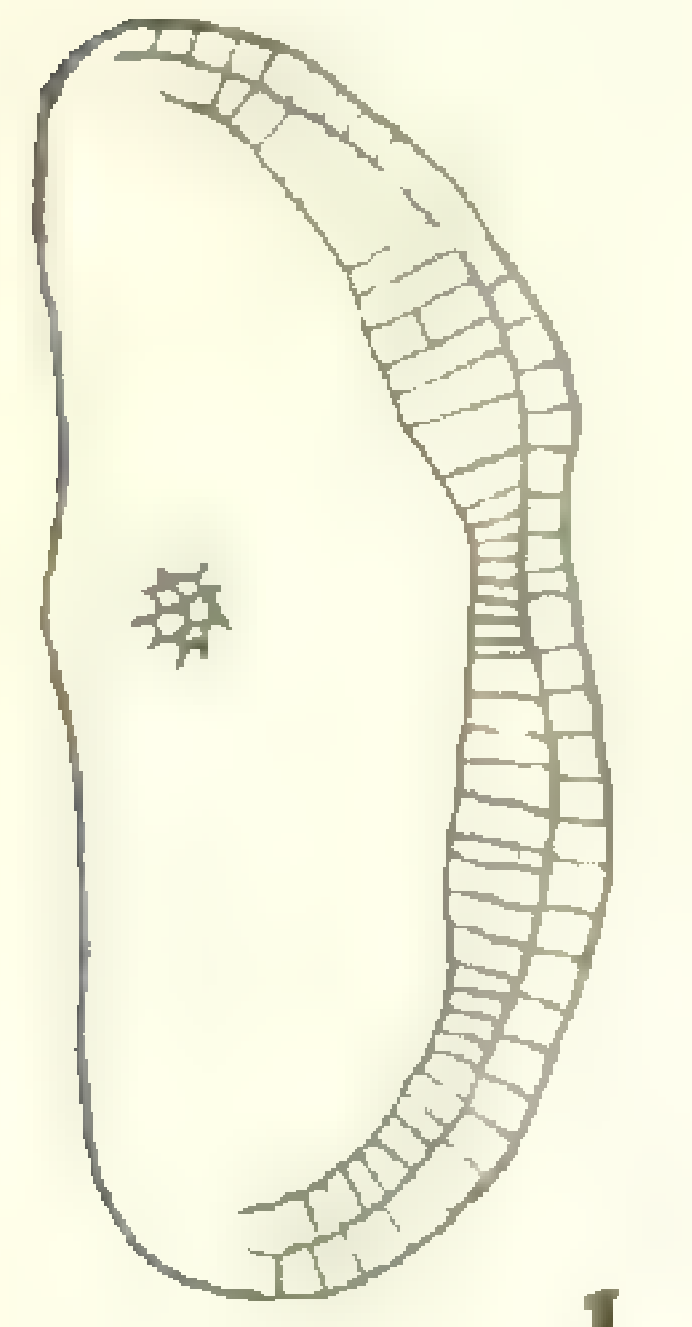
I wish to acknowledge my indebtedness to Dr. John M. Coulter and Dr. Charles J. Chamberlain for their kindly direction and valuable suggestions.

HULL BOTANICAL LABORATORY,
THE UNIVERSITY OF CHICAGO.

NOTE.—Just as this paper goes to press, one by Professor Strasburger, *Einige Bemerkungen zu Pollenbildung bei Asclepias* (Ber. deutsch. bot. Gesells. **19**: 450–454. 1901), dealing with *Asclepias Cornuti* and *Cynanchum Vincetoxicum*, has come to hand, confirming in a general way the results reported above.

EXPLANATION OF PLATE XIII.

The figures are reduced to one half their original size. The lenses used were Leitz objectives 3 and 7, and Zeiss $\frac{1}{12}$ oil immersion; oculars, Reichert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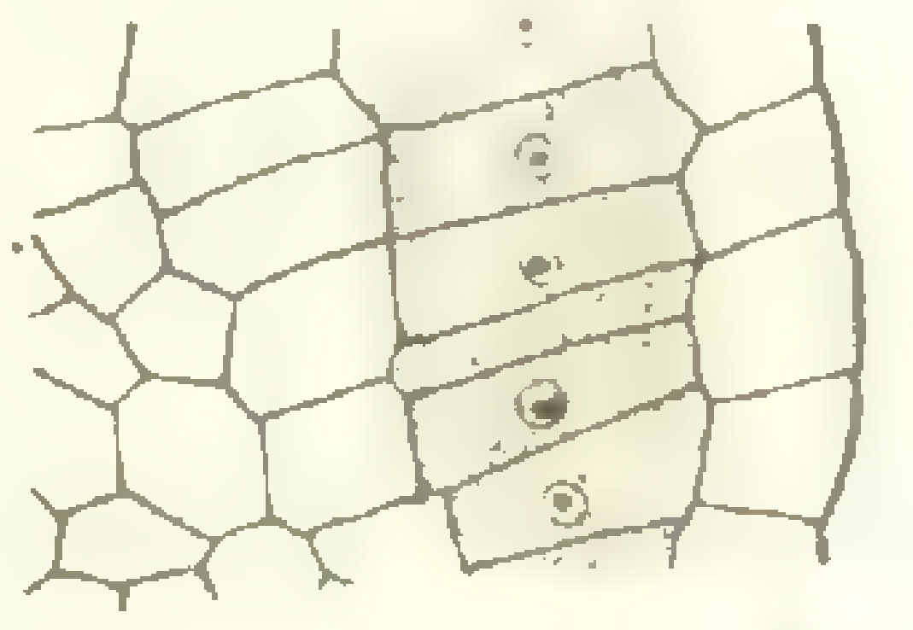
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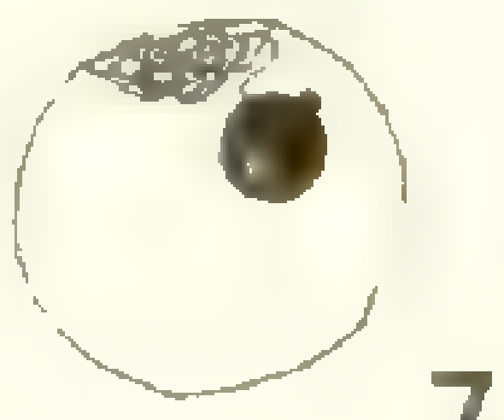
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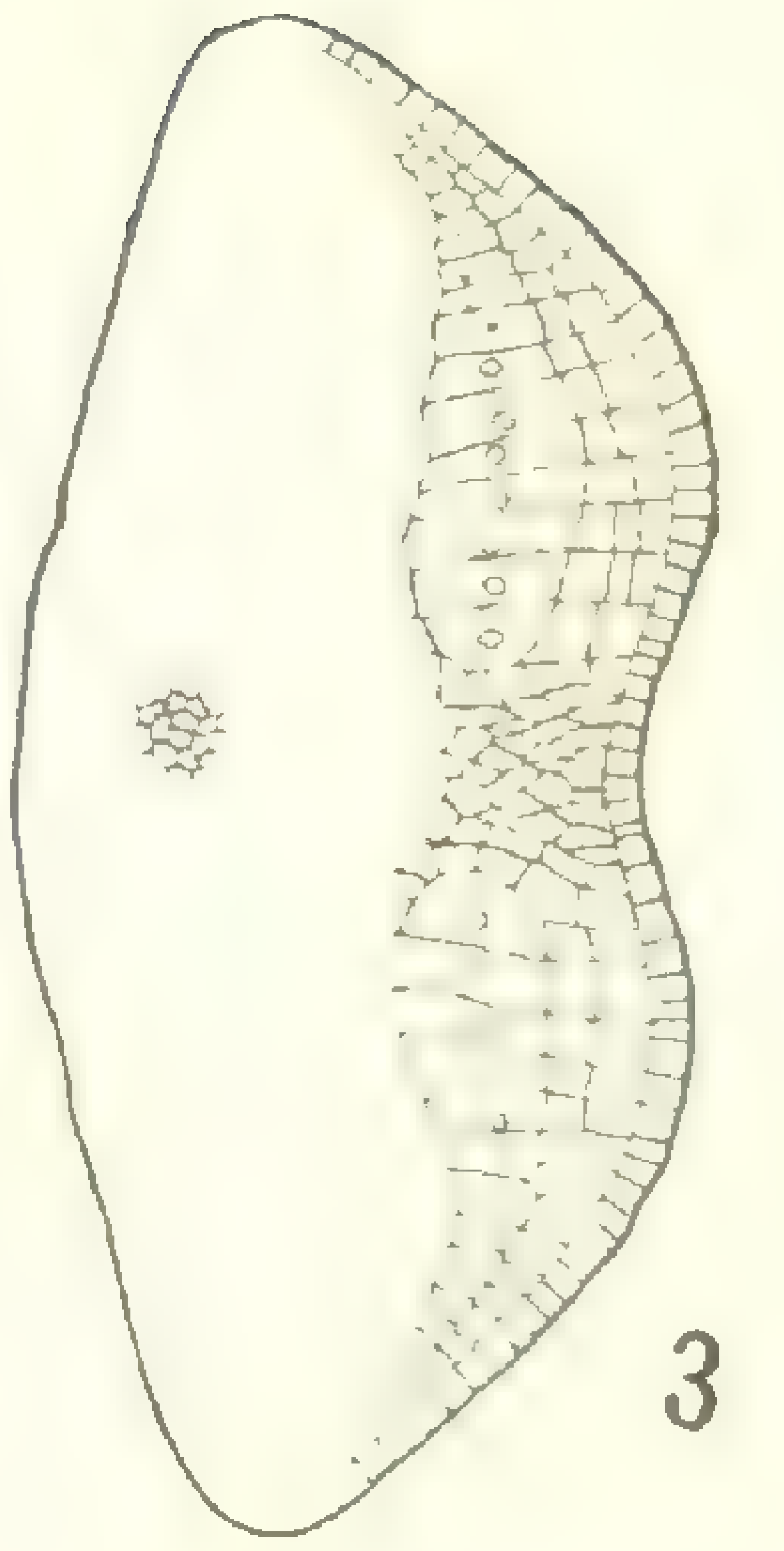
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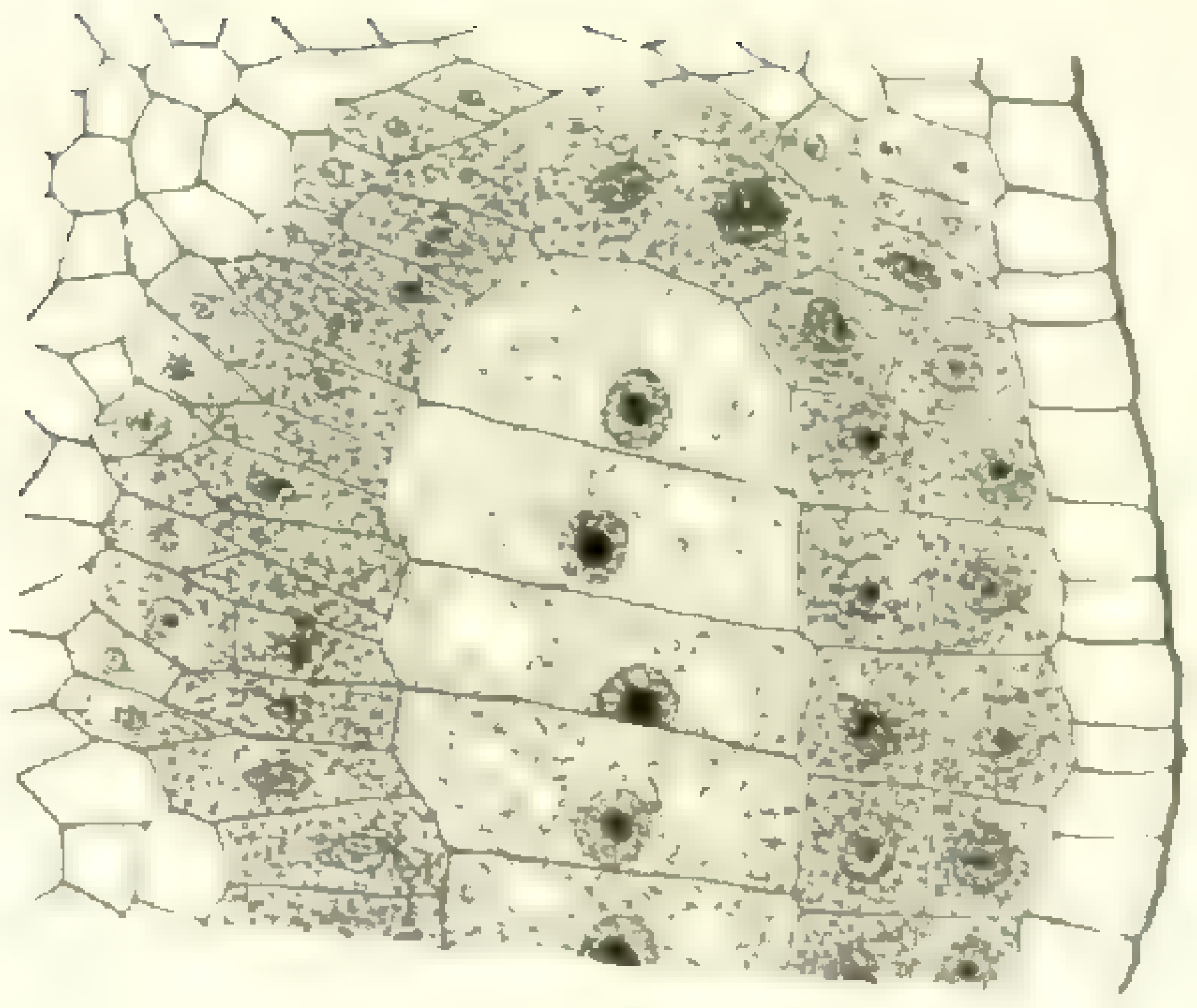
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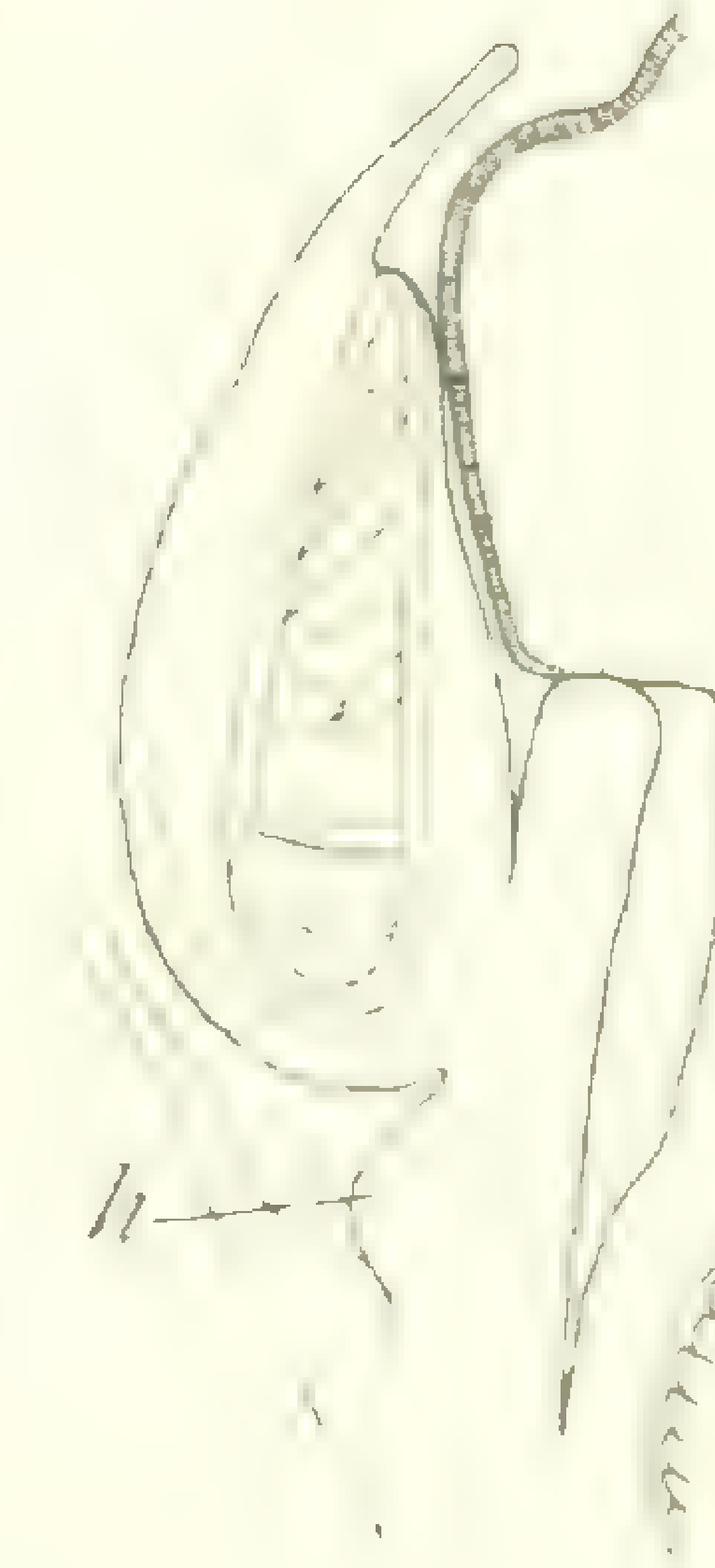

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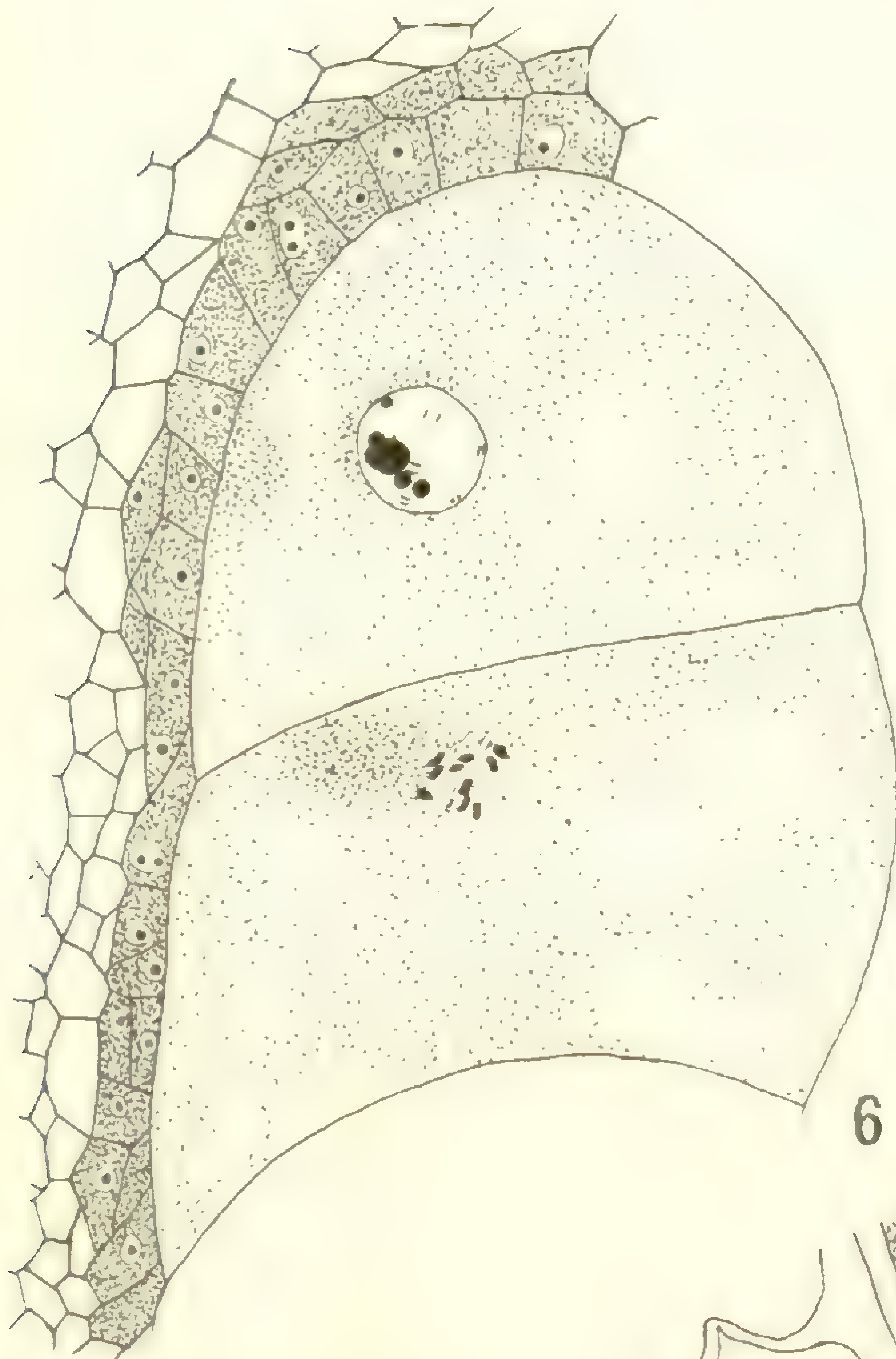
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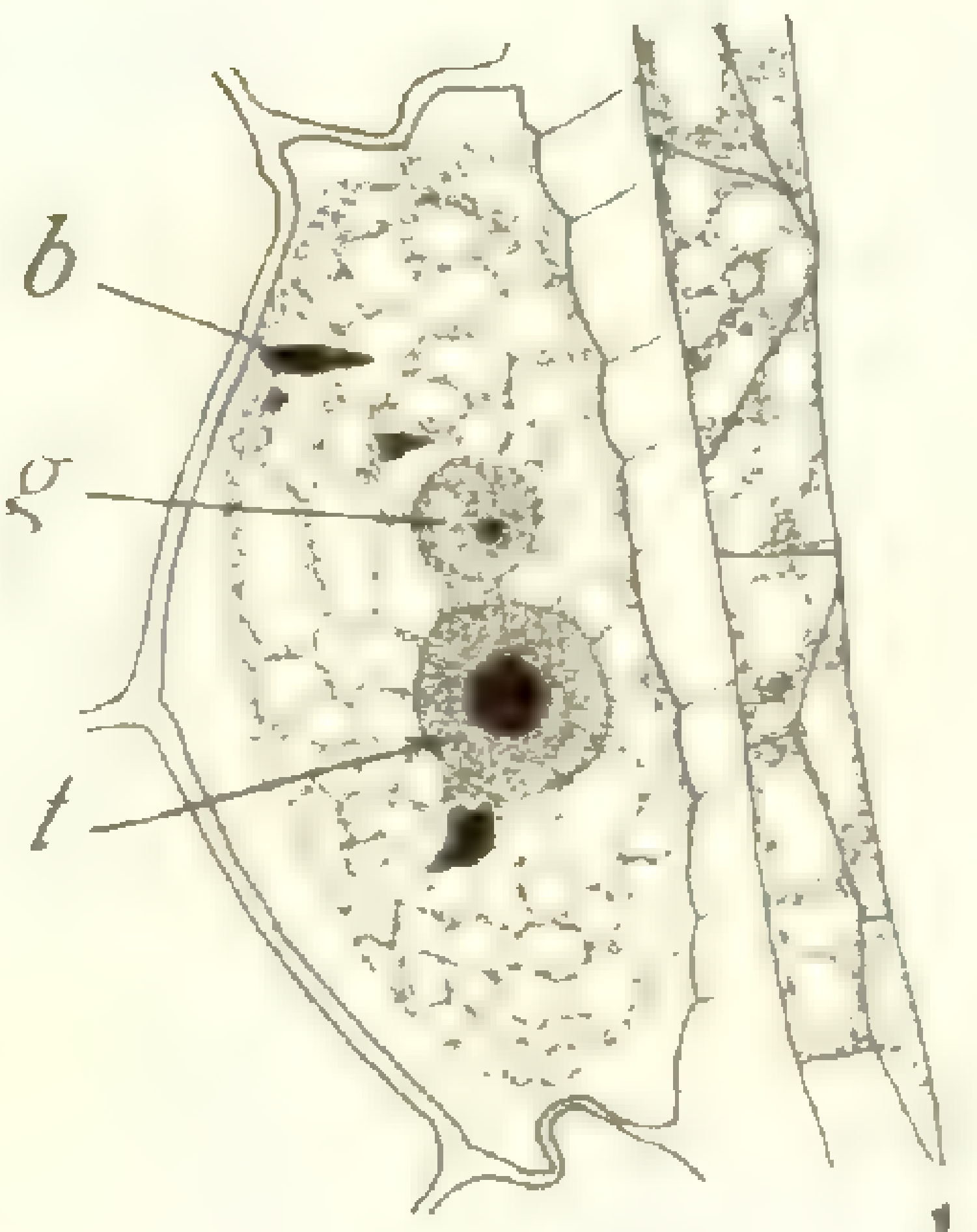

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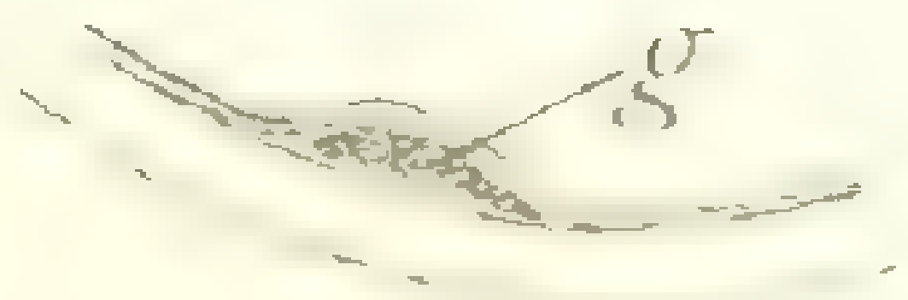

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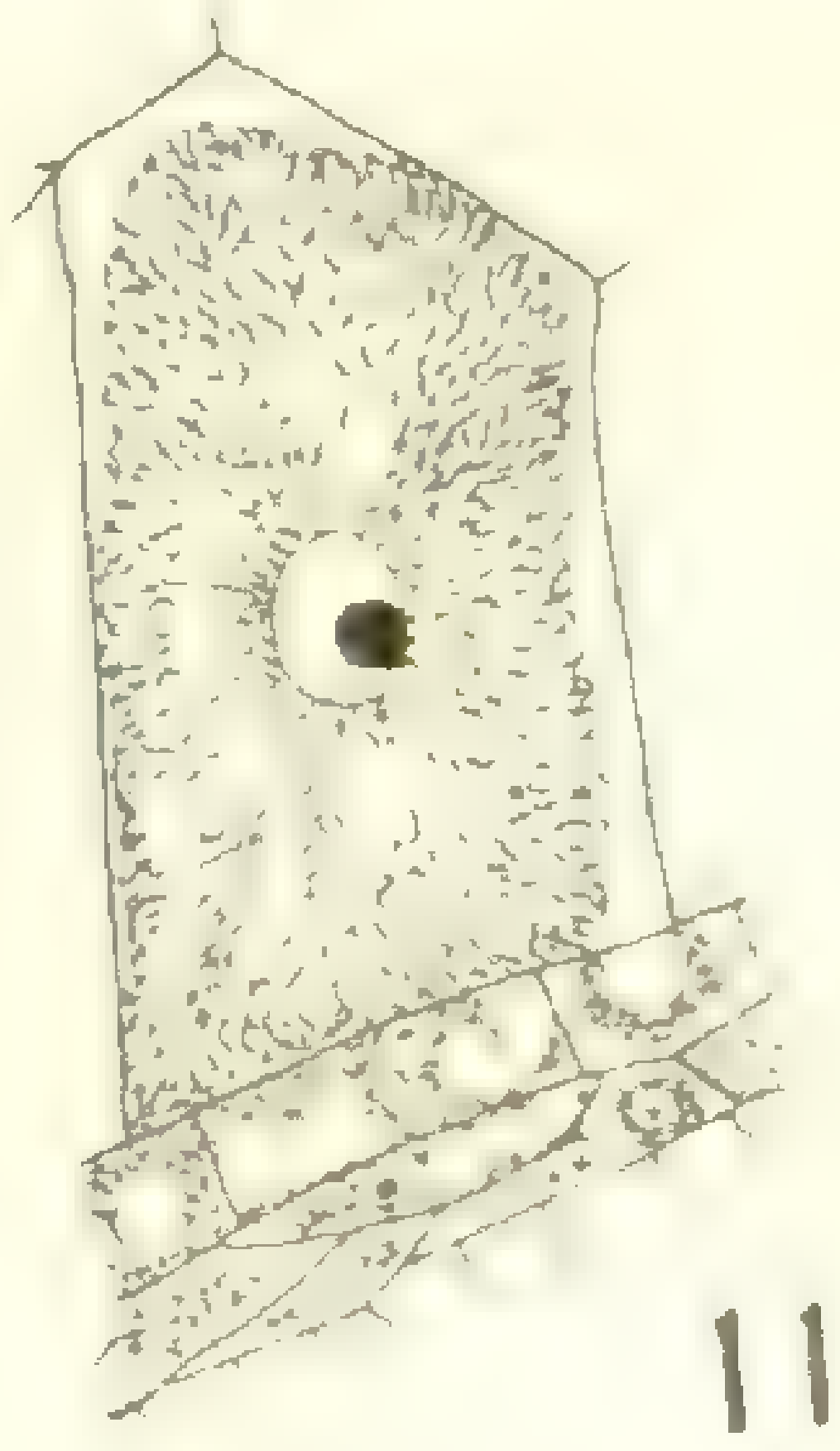
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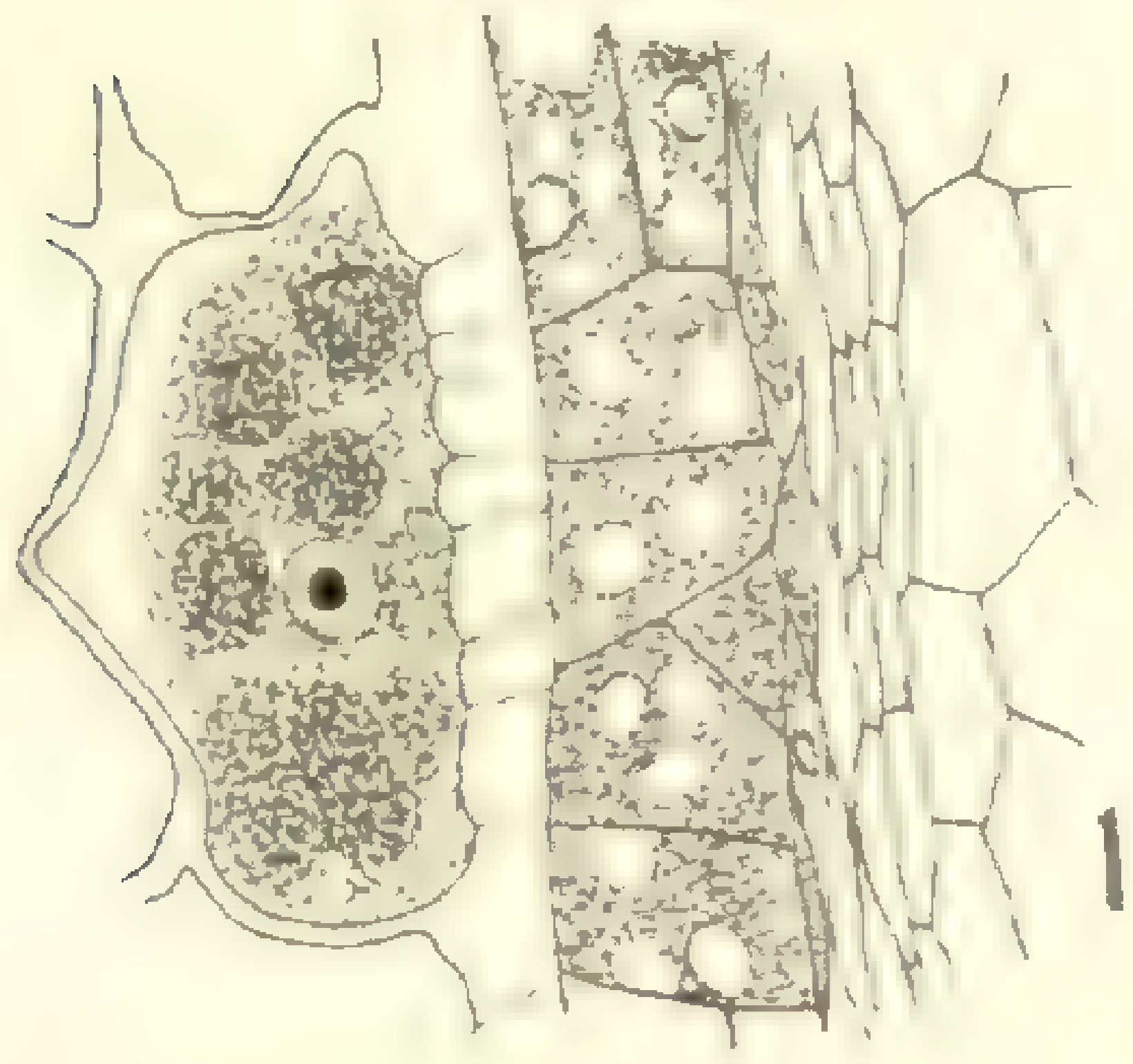
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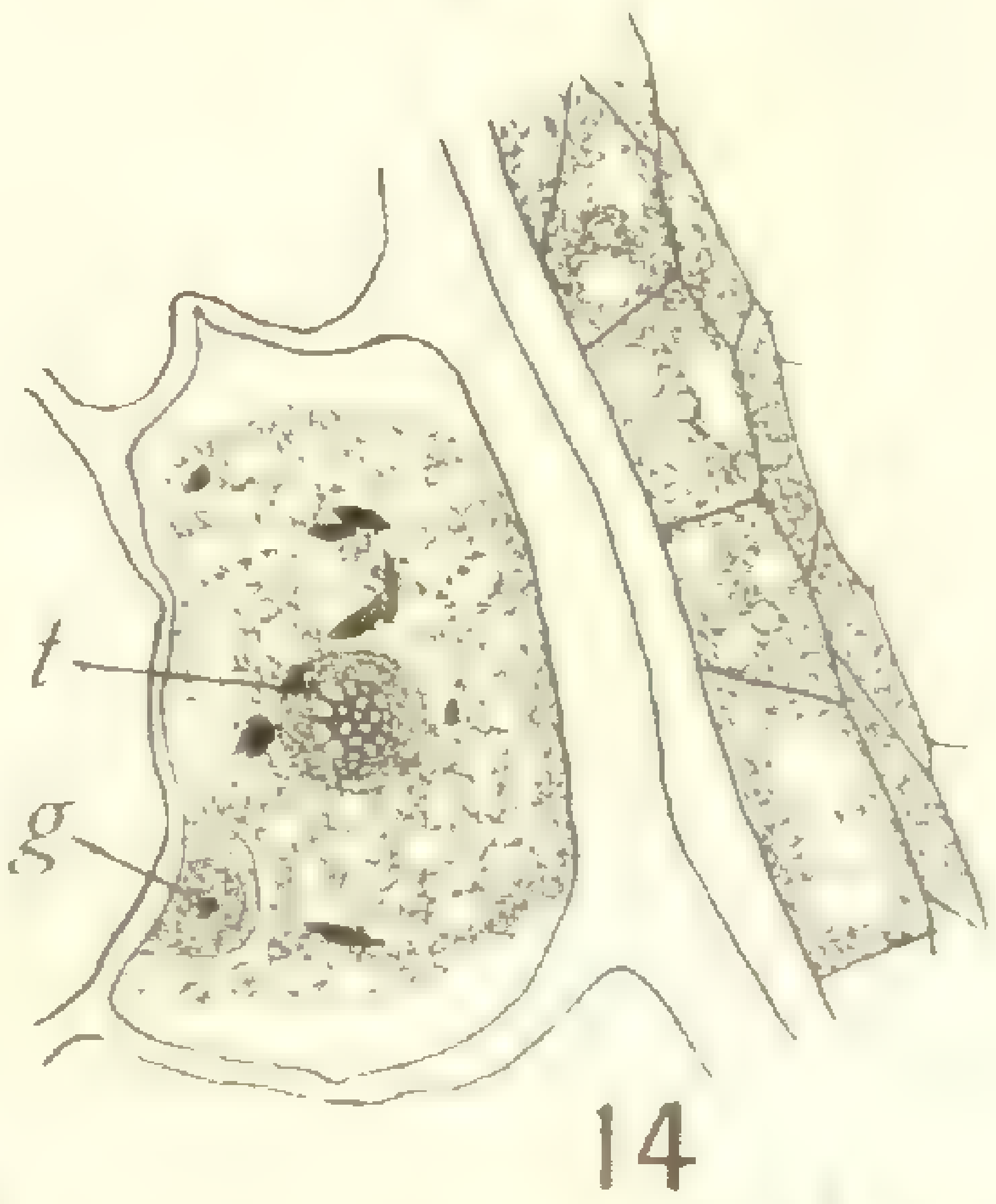

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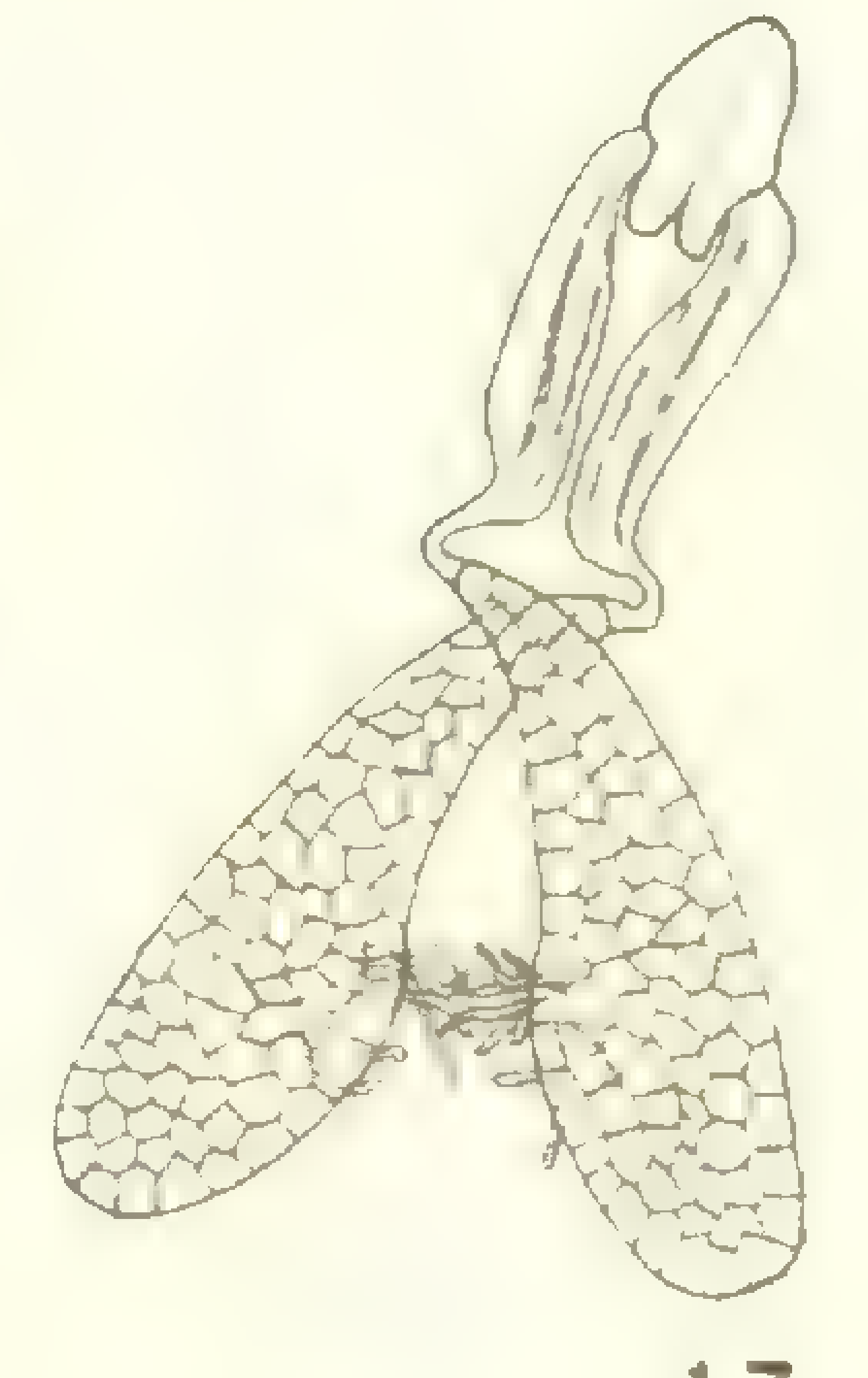
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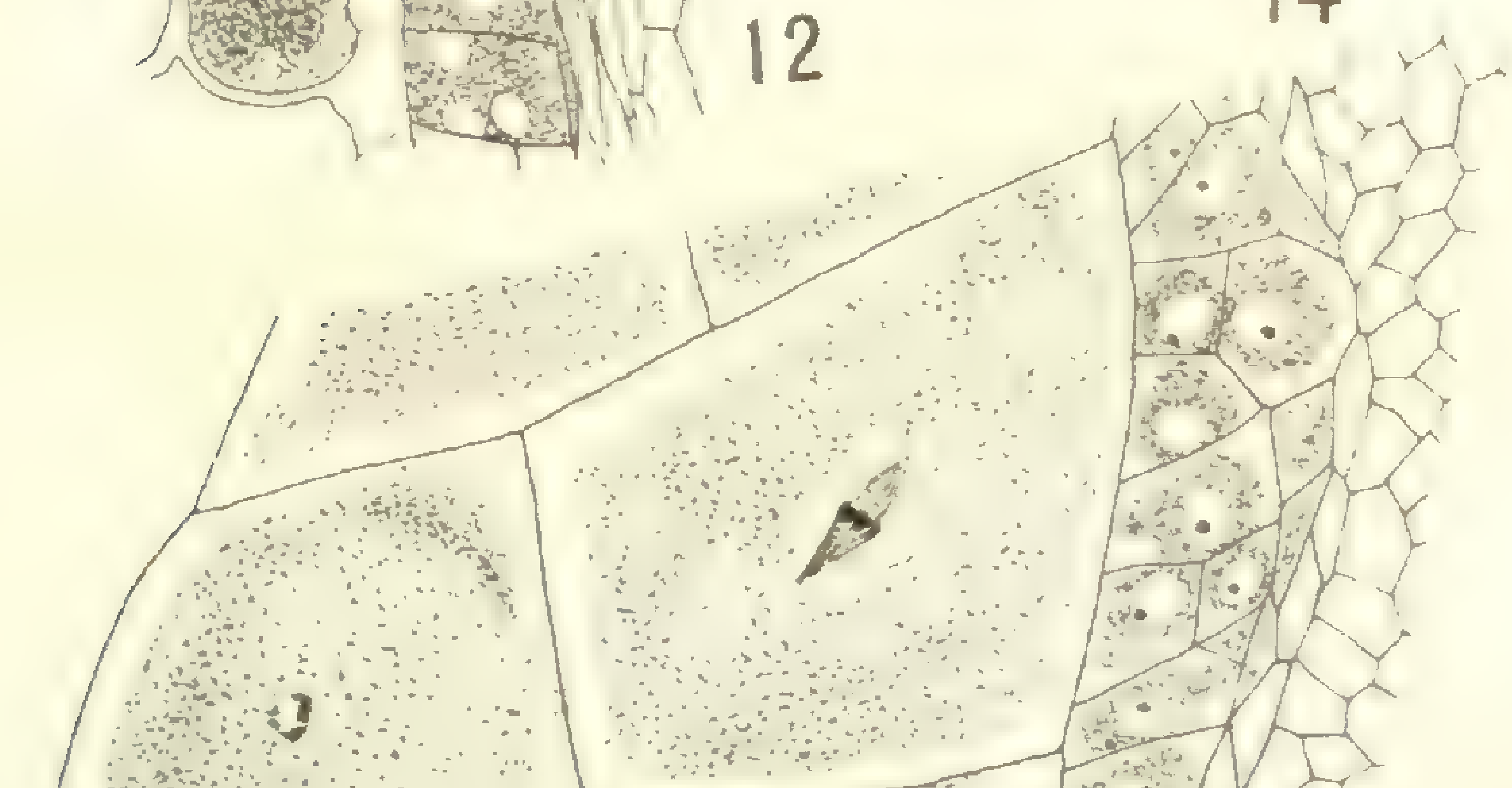
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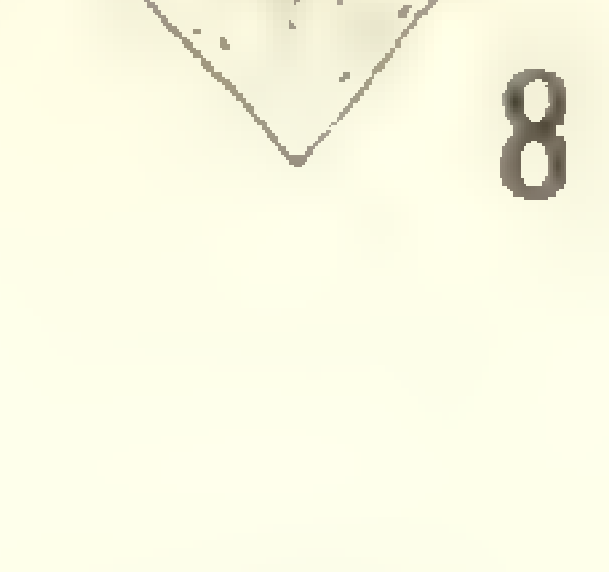
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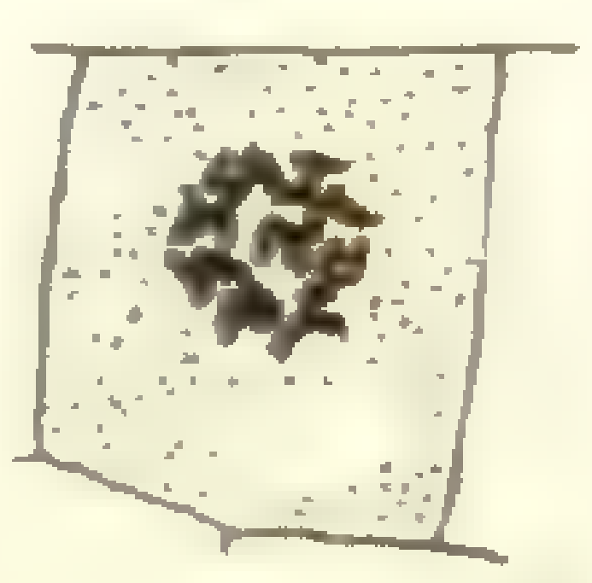
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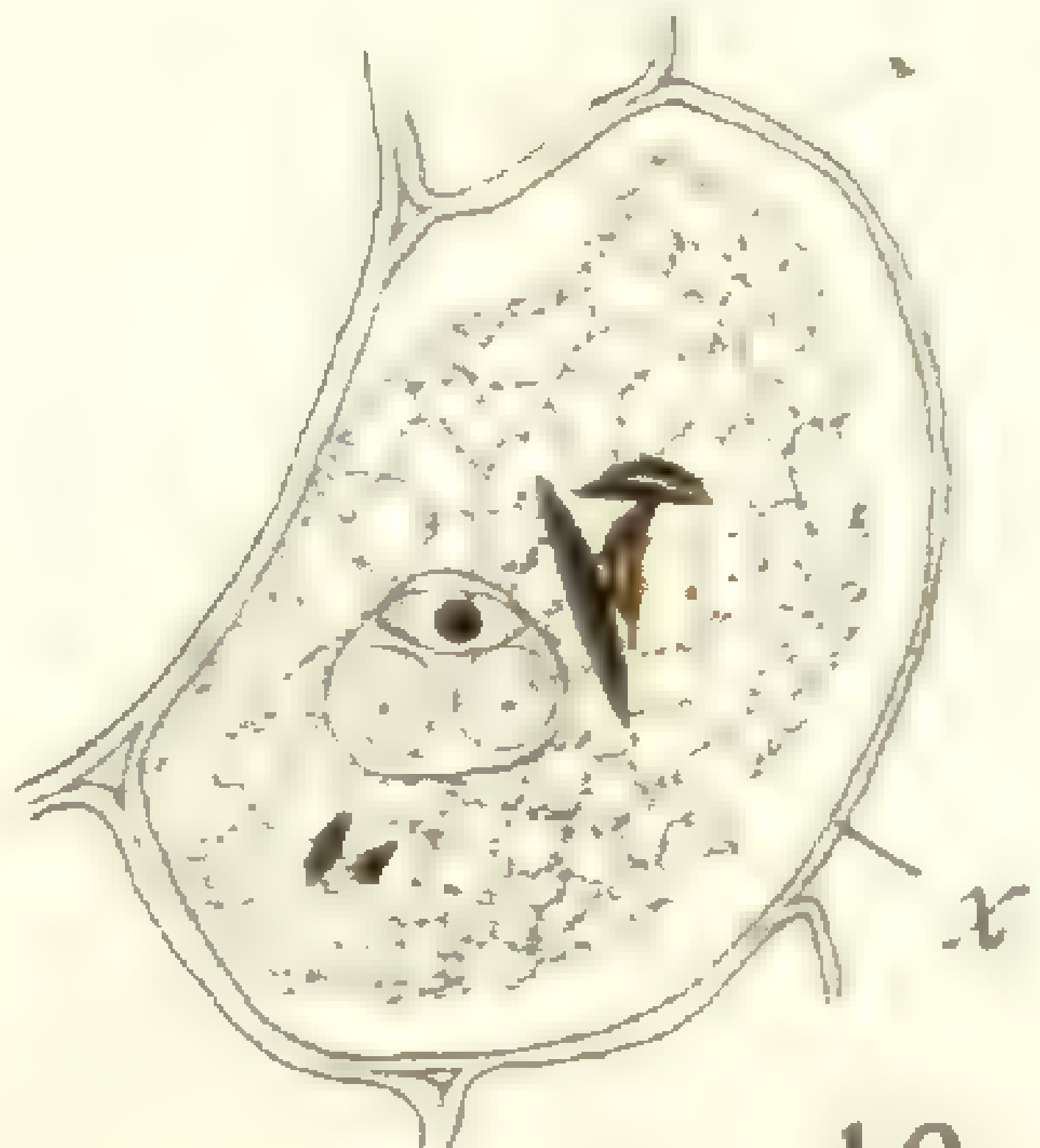

16

FRYE on POLLEN OF ASCLEPIAS

1 and 2, and Zeiss compensating 4, 8, 12, and 18. All drawings were sketched with a Bausch and Lomb camera lucida.

Figs. 1–4. Asclepias Cornuti.

FIG. 1. Cross section of young stamen showing archesporium just beginning the division into primary wall and primary sporogenous layers; somewhat diagrammatic. × 290.

FIG. 2. Part of *fig. 1*, through archesporium. × 800.

FIG. 3. Section across a stamen showing primary sporogenous cells grading into vegetative cells and division of primary wall layer into four layers; partly diagrammatic. × 290.

FIG. 4. Part of *fig. 3*, showing tapetal nature of cells surrounding the primary sporogenous cells. × 800.

Figs. 5–16. Asclepias tuberosa.

FIG. 5. Longitudinal section through stamen showing location of sporangium and orientation of cells within; *h*, hood; partly diagrammatic. × 22.

FIG. 6. Longitudinal section of lower part of sporangium; two spore mother cells undergoing first division; one nucleus in aster stage, the other with chromosomes just split. × 800.

FIG. 7. Synapsis stage of nucleus in spore mother cell. × 800.

FIG. 8. Aster stage in division of a vegetative cell. × 2150.

FIG. 9. Axial view of plate of chromosomes in aster stage in vegetative cell. × 2150.

FIG. 10. Longitudinal section of sporangium near its top showing second division of nucleus of spore mother cell. × 800.

FIG. 11. Section of young microspore showing thready protoplasm; tapetal cells adjacent. × 800.

FIG. 12. Section of microspore containing masses of denser ptotoplasm; walls already thickened; tapetum adjacent. × 800.

FIG. 13. Section of microspore; *b*, deeply staining bodies; *g*, generative nucleus; *t*, tube nucleus.

FIG. 14. Section of microspore showing generative nucleus (*g*) flattened against the wall of the cell and just cut off. × 800.

FIG. 15. Section of a generative cell cut off from the rest of the microspore by a considerable wall. × 900.

FIG. 16. Section of microspore containing what may be a fragmented tube nucleus; *x*, side torn from pollinium wall. × 800.

Fig. 17. Asclepias incarnata.

FIG. 17. Sketch of two pollinia germinating in a 10 per cent. solution of cane sugar; partly diagrammatic. × 45.

ON THE DISTRIBUTION OF RED COLOR IN VEGETATIVE PARTS IN THE NEW ENGLAND FLORA.

F. GRACE SMITH.

THE meaning of red color in the vegetative parts of plants is a subject which very early attracted attention. Beginning with Grew (1677), many observations and experiments have been made, resulting in several theories. Von Mohl[1] (1837) was the first of modern botanists to study the subject with thoroughness, concluding, according to Overton's review of his work, that red color is an incidental result of cooler temperature and intense light. Kuntze[2] (1877), on the other hand, gave an ecological significance to red color, considering it a protection against animals. Stahl[3] (1888) showed that animals usually choose green leaves first, but if hungry eat either green or red leaves. Since this happens in the dark as well as in the light, some difference in the nourishing qualities or in the taste of the red leaves seems to be the determining factor of the choice. Pick[4] (1883), according to Stahl, held the theory that red color favors the breaking up and change of starch into sugar, by absorbing the light rays injurious to this change. Kerner[5] thought the intense light is harmful to the plant, being destructive to young chlorophyll, and that the red color forms a screen, thus permitting the change and passage of food materials. Engelmann[6] (1886) gave no positive meaning to erythrophyll, for it seemed sufficient to him that assimilation takes place, but little retarded by the loss of light. Stahl[7] (1896) agreed with Kerner and Pick in the belief that the red color is a device for promoting the change and passing of food stuffs, not however in its use as a light screen, but by raising the temperature of plant tissues through its property of converting light into heat; cold delays these processes. This warming up of the plant also favors transpiration, an ecological factor as important in Stahl's view as the one mentioned. Overton[8] (1899) presented the theory that the red color is a glucoside compound, produced as a result of sugar concentration in the cell, under the influence of intense light and cool temperature. He assigned no distinct ecological significance to red color and in reality gave us a theory which is a modification of Von Mohl's. MacDougal[9] (1896) has given a good popular account of the theories concerning red color.

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[1] Untersuchungen über die winterliche Färbung der Blätter. Included in Vermischte Schriften 375–392.

[2] Schutzmittel der Pflanzen gegen Tiere und Wetterungunst. Gratisbeilage zur Bot. Zeit. Leipzig, 1877.

[3] Pflanzen und Schnecken. Jenaisch Zeitsch. Nat. u. Med. **22**.

[4] Bedeutung des rothen Farbstoffs bei den Phanerogamen und die Beziehung desselben sur Stärkewanderung. Bot. Centralbl. **16**: 281.

[5] Natural History of Plants (transl. by Oliver) **1**: 101–103, 364–366, 483–499.

[6] Die Farben bunten Laubblätter und ihre Bedeutung für die Zerlegung der Kohlensäure im Lichte. Bot. Zeit. **45**: 449.

Little attention has been given to the study of red color in the eastern United States. Stahl and Overton cite this region with the Alps as offering the best conditions by far for a great display of color. No attempt, so far as I can find, has been made anywhere to study comprehensively the red color in summer foliage, or, in fact, to work up the subject at all in a statistical way, and therefore with a view to seeing how far statistical observations made in New England may agree with the principal theories this study is offered. Thanks are due to Mr. M. L. Fernald, of the Gray Herbarium, for naming many plants, and to Dr. W. F. Ganong, of Smith College, with whose kind assistance and direction the working out of the data was done.

The plants examined were gathered at random in Northampton and vicinity, Springfield, Warren and Woods Hole, Mass., and in Squirrel island, Maine. The proportion of situations, dry and wet, shady and sunny, from which the specimens were taken was about the same. At first only those plants were

[7] Ueber bunte Laubblätter. Ann. Jard. bot. Buit. **13**: 137.

[8] Beobachtungen und Versuche über das Eintreten von rothen Zellsaft bei Pflanzen. Prings. Jahrb. **33**: 171.

[9] Physiology of color in plants. Pop. Sci. Monthly **49**: 1.

noted which showed red color. After most of the data were taken it was realized that the number of specimens lacking red color, but growing in the same situations, was needed for comparison, especially for determining what per cent. of our flora showed red color and what situations produced the greatest proportion of cases. Last summer a record was kept of the number of plants found on Squirrel island, Maine, an island two or three miles in circumference. The total number was 126, of which 102 showed red color ; 24 showed *none at that time*, 5 of them being evergreens. Most of these 24 plants were recorded red at other times in other places. These figures, though true for a very limited region, give evidence that red color is more widely prevalent than would be supposed.

The data taken gave the name of the place, situation in which the plant was gathered, whether roadside or woods, whether wet or dry, the amount of shade, height of the plant, part colored, the date, and, as far as was ascertainable by microscopic examination, in what tissues the red color was located. The fact should be emphasized that the date at which the plant was gathered made a decided difference in the color. Owing to the length of the records taken only the results are given here.

In analyzing the results, attempt has been made to think of every possible interpretation of the presence of the color, and to ascertain by percentage how many specimens confirm each.

The first records consider *the part* of the plant in which the red occurs. Of 285 plants showing red, the stem has 211 cases (73.3 per cent.), the petiole 140 (49.1 per cent.), the leaf (mesophyll) 99 (35 per cent. of which 7 per cent. were young leaves), and the veins 66 (23 per cent.). Red color, therefore, is more common in stems than in leaves.

In upright stems more red, or red only, was shown evenly distributed in 138 cases (65.4 per cent.), near the ground in 31 (14.7 per cent.), at the nodes in 23 (10.9 per cent.), at the tip in 3 (1.4 per cent.). Red color, therefore, is not commonly localized, but evenly distributed. Cases where more red was shown on one side of an upright stem than on another were found to be where light was brighter on the red side.

In creeping stems and inclined branches there was more red on the upper surface in 12 cases (5.7 per cent.), and on the lower surface in one case (1 per cent.).

Of 140 *petioles* more red was shown on the upper surface in 53 cases (38 per cent.), evenly distributed in 46 (32.8 per cent.), near the base in 39 (28 per cent.), on the lower surface in 10 (7.1 per cent.), near the blade in 5 (3.5 per cent.). In petioles, therefore, red color is most frequent on the upper surface, but nearly as often evenly distributed, while some petioles show a tendency to color toward the base.

Of 65 *veins* more red was shown evenly distributed in 32 cases (49.2 per cent.), on the upper surface in 18 (27.7 per cent.), on the lower surface in 15 (23.1 per cent.). It follows, therefore, that in veins, as in stems, the red color is evenly distributed in the majority of cases, and that there is more color on the upper than on the lower surface.

Of 99 *leaves* (mesophyll) more color was shown evenly distributed in 33 cases (33.3 per cent.), on edge in 20 (20.2 per cent.), on upper surface in 18 (18.1 per cent.), at tip (mostly young) in 15 (15.1 per cent.), on lower surface in 14 (14.1 per cent.), at base near petiole in 11 (11.1 per cent.). The conclusions, therefore, are that cases of even distribution are in the majority; that there is more color on the upper than on the lower surface, and on the edge than near the tip.

In a large number of cases the red color was seen on flower stems, bracts, and scales, but because these could not be ascertained for all plants the results were not tabulated. Buds, stipules, spines, tendrils, and a few roots were also found colored red. Out of the 285 specimens 26 were streaked or mottled in some way.

The next records consider the color distribution in relation to external conditions, as light, etc. Of the 285 plants examined 150 (52.6 per cent.) were gathered in dry sunny places, 61 (21.4 per cent.) in dry shady places, 40 (14 per cent.) in wet sunny places, 34 (12 per cent.) in wet shady places. Dry situations, therefore, result in more color than wet ones; sunny situations in more than those that are shady; dry and sunny have far the most of all; and wet shady the least of all.

Of 211 *stems* 120 (56.8 per cent.) showed red in dry sunny places, 44 (20.8 per cent.) in dry shady places, 31 (14.7 per cent.) in wet sunny places; 16 (7.6 per cent.) in wet shady places.

Of 140 *petioles* 70 (50 per cent.) showed red in dry sunny places, 31 (22.1 per cent.) in dry shady places, 22 (15.8 per cent.) in wet shady places, 17 (12.1 per cent.) in wet sunny places.

Of 65 *veins* 31 (47.7 per cent.) showed red in dry sunny places, 14 (21.5 per cent.) in dry shady places, 12 (18.5 per cent.) in wet sunny places, 8 (12.3 per cent.) in wet shady places.

Of 99 *leaves* (mesophyll) 48 (48.4 per cent.) showed red in dry sunny places, 19 (19.1 per cent.) in dry shady places, 18 (18.1 per cent.) in wet shady places, 14 (14.1 per cent.) in wet sunny places.

The proportion of red in the parts of the plant is about the same for the plant itself; greater number of cases in dry places than in wet; in dry sunny places the largest percentage of all. Dry shady and wet shady places showed about the same number of cases.

An interesting confirmation of these percentages is found in reckoning them theoretically. For example, if 21.4 per cent. of the 285 plants were found growing in dry shady places, out of the 211 specimens showing red on the stem 45 should show it in dry shady places; and 40 did show it.

In dry shady places the numbers expected and attained were as follows: stems 45–44; petioles 30–31; veins 13–14; leaves (mesophyll) 21–19.

In dry sunny places the numbers expected and attained were as follows: stems 111–120; petioles 73–70; veins 33–31; leaves (mesophyll) 52–48.

In wet shady places the numbers expected and attained were as follows: stems 21–16; petioles 17–22; veins 7–8; leaves (mesophyll) 13–18.

In wet sunny places the numbers expected and attained were as follows: stems 33–31; petioles 19–17; veins 8–12; leaves (mesophyll) 13–14.

In sunny places the number of red stems is considerably larger than expected, and in wet shady places the number of red leaves is larger; otherwise the numbers expected and attained are about the same. Percentages might also be worked out for the number of specimens showing red on the stems, near the ground, at joints, etc.

In addition to the 285 plants, records were taken for 234 duplicates growing in the following situations: 129 in dry sunny places, 44 in dry shady places, 35 in wet shady places, 26 in wet sunny places. This accords with the main series except in the exchange of wet shady and wet sunny places.

To determine if the red color present in the spring and summer is a persistence of the early spring coloration, or a new feature, 109 plants were marked in the spring in different localities with copper tags. Plants were marked only when others of the same species near by were red. These were examined in summer and again in the fall, and changes recorded. One hundred plants were recorded the three times, although in some cases the marked specimen was lost and data were taken from neighboring plants of the same kind. In 54 cases red color was lost in some part; in 34 there was no appreciable change; in 28 red color was gained in some part; in 21 it was lost entirely. There was no attempt to tell how many plants without color in spring gained it during the summer or fall.

Of the 54 plants in which the red color was lost there were 36 cases (66.6 per cent.) in the leaf (mesophyll), 13 (24 per cent.) in the petiole, 12 (22.2 per cent.) in the veins, and 11 (20.3 per cent.) in the stem. Color was gained in 14 cases (50 per cent.) in the petiole, in 9 (32.2 per cent.) in the stem, in 6 (22.2 per cent.) in the veins; in 2 (7.1 per cent.) in the leaf (mesophyll).

Therefore, red color cannot be simply a persistence of spring coloration, nor is it simply an addition in the fall, for of 28 cases of additional color 18 occurred in the summer and 10 in the fall. Color is more often lost in the leaf than in the stem, the cases of its persistence in the leaf through summer and fall being 8, of its loss 36. The percentage of increase in color is greater in stem and petiole than the loss; it is less in the leaf blade; and about the same in the veins. In order to determine in what tissues the red color is present, examination of 207 plants was made with the microscope. The following tables give the results:

		Stem.			Petiole.			Leaf-blade.			Veins.		
Epidermis		78			35			41			12		
Cortex	Hypodermis	38	66	136	29	47	97	15	18	55	5	9	25
	Collenchyma	28			18			3			4		
	Parenchyma	65	70		49	50		37	37		16	16	
	Sclerenchyma	5			1			0			0		
Stele	Vasc. bundles	3	15		1								
	Pith	12											

DRY, SHADY PLACES.

		Stem.			Petiole.			Leaf-blade.			Veins.		
Epidermis		9			6			4			0		
Cortex	Hypodermis	8	11	26	8	10	19	2	2	11	1	1	3
	Collenchyma	3			2			0			0		
	Parenchyma	13	15		9	9		9	9		2	2	
	Sclerenchyma	2			0			0			0		
Stele	Vasc. bundles	1	6		0								
	Pith	5			1								

DRY, SUNNY PLACES.

		Stem.			Petiole.			Leaf-blade.			Veins.		
Epidermis		48			18			20			6		
Cortex	Hypodermis	18	33	62	9	18	37	8	10	26	3	4	8
	Collenchyma	15			9			2			1		
	Parenchyma	29	29		19	19		16	16		4	4	
	Sclerenchyma	0			0			0			0		
Stele	Vasc. bundles	1	4										
	Pith	3											

WET, SUNNY PLACES.

		Stem.			Petiole.			Leaf-blade.			Veins.		
Epidermis		15			7			10			6		
Cortex	Hypodermis	10	18	33	8	13	23	3	4	9	1	4	12
	Collenchyma	8			5			1			3		
	Parenchyma	13	15		9	10		5	5		8	8	
	Sclerenchyma	2			1			0			0		
Stele	Vasc. Bundles	0	2										
	Pith	2											

WET, SHADY PLACES.

		Stem.			Petiole.			Leaf-blade.			Veins.		
Epidermis		6			4			7			0		
Cortex	Hypodermis	2	4	15	4	6	18	2	2	9	0		
	Collenchyma	2			2			0			0		
	Parenchyma	10	11		12	12		7	7		0	2	
	Sclerenchyma	1			0			0			2		
Stele	Vasc. bundles	1	3		1								
	Pith	2											

DISAPPEARANCE OF COLOR IN 54 PLANTS.

		Stem.		Petiole.		Leaf-blade.		Veins.	
Epidermis		3		7		22		6	
Cortex	Hypodermis	7	12	5	13	3	21	2	10
	Collenchyma								
	Parenchyma	5		8		18		8	
	Sclerenchyma								
Stele	Vasc. bundles								
	Pith	2		0		0		0	

In frequency of color epidermis exceeds hypodermis or parenchyma in stem and leaf-blade, but in each case the cortex shows the largest number of cases. In dry sunny places the epidermis has most color, the color gradually disappearing in the stem from the outside in. In dry shady and wet shady places the parenchyma exceeds, in wet sunny places the hypodermis or epidermis. It seems then as if sunlight tends to increase the red color in the epidermis or hypodermis. In cases of disappearance of color, the loss is greatest in the epidermis of the leaf-blade, and in the cortex of stem and petiole. In 26 cases of loss, the conditions had changed since spring from sunny to shady. This would make it seem as if red might be a protection from intense sunlight, but in 28 cases of appearance of color 13 were found in conditions which had changed from sunny to shady, and 5 were found in conditions which had changed from wet to dry. One might conclude that change of conditions favors change in color, from green to red or red to green, as has been asserted by others.

Most of the plants with red color were gathered in dry sunny places. This does not accord with observations of Stahl, who finds in moist or shady places the most noticeable red coloring. His theory does not seem applicable to the facts just given, for the conditions of sunlight and warmth in this case favor photosynthesis and conduction, also transpiration. The percentage is so large it could not be due to collecting more specimens in the spring or fall, when the temperature is lower, and thus be due to increased sugar concentration according to Overton's theory.

Taking the whole number of cases, the red color gives the largest percentages for stems and petioles, really the conducting parts of the shoot. One might think with Stahl that some advantage is derived from red color in photosynthesis and passage of food material, but again why this is needed in most of these cases is not so clear, since conditions were already sufficiently favorable for transpiration, etc. The large amount of color in the cortex seems to favor Stahl's theory also. If we apply Pick's theory, that the red color protects the conducting parts from the injurious effects of light upon the changing substances in them, we seem to have a strong argument in its favor, for the majority of the cases noted were recorded in dry, sunny places.

In wet shady places only is the percentage of cases of red color in the leaves greater than in the stems and veins. In Stahl's paper most attention is paid to color in leaves, so here is an agreement, if only a slight one, with his theory of the need of warmth to increase transpiration.

In stems, petioles, veins, and leaf-blades the largest percentages are for an even distribution of red color upon the surfaces of these parts. This would seem to show either that the shoot was evenly lighted or that some factor other than sunlight was the determining one in causing red color. However, the upper surfaces of the leaves, veins, and petioles show more color than under surfaces, and this accords with observations of others. Kerner's theory of protection from too great light, and Stahl's of increasing transpiration through the aid of red, apply here, although it is hard to see, as said before, why there is need of greater photosynthesis than is brought about by naturally favorable conditions. Overton's view is not applicable, for cool temperature is certainly not a factor in the conditions. The disappearance of red color in leaves when greater shade is present, and the great number of cases where red is located in the epidermis, are favorable to Kerner's theory of protection.

Another fact agreeing with the latter theory is in the case of upright stems, where one side, the side always toward the sun, shows often the more color. This was noticed continually in Ambrosia.

The red color is intensified at the joints of stems and petioles. This deepening of color, as well as that upon the upper surface of parts, is greatest in proportion in plants growing in wet shady situations. The theory of Stahl applies here, for the passing of food materials may be checked somewhat at the joint, where tubes pass into the stem; but Overton's theory applies just as well, since conduction is delayed here and sugar must be concentrated in the cells of this region. Cool temperature does not appear here however. Any theory of protection from light is not applicable, since the joints are as much shielded as the other parts of the shoot.

A large number of cases were found where the stem was very red near the ground. None of the theories seem to fit this fact.

Cases where color is absent just at the joints and present upon the rest of the stem, where petioles are red near the blade only, where old tendrils are very red, where color is present in the hairs of leaves and not in the leaf surfaces, are unexplained by any theory; also the appearance of red under the same conditions which usually favor the disappearance of color.

Stahl has given a plausible explanation of color in plants of the moist tropics, where color is located in the cells of tissues near the surface. Overton explains autumnal and spring coloration, but finds, although he can produce color in internal tissues of the plant, he is seldom able to do so in epidermal layers. None of the explanations given apply to all the cases here recorded.

In conclusion it is seen that the statistical observations presented fit no one theory in all particulars. Some facts agree with no theory at all so far as known. The suggestion may be made that with further experimental study red color may be found subserving a number of purposes or having a number of different meanings; or, on the other hand, it may be due to an entirely unknown cause which may fit all cases.

Botanical Laboratory, Smith College,
Northampton, Mass.

SOME PLANT ABNORMALITIES.[1]

GEORGE HARRISON SHULL.

THE investigation of the abnormal, either in the structure or function of organisms, is often of great value in arriving at correct interpretation of normal conditions. But any specific abnormal form is rare as compared with the frequency of the normal condition, and as no one observer is likely to discover a great number of cases, it is important that all should be recorded.

Already botanists have described very many instances of abnormal plant forms, so that the bibliography of plant teratology is already extensive. Thus Penzig[2] (1894) gives several thousand references to described cases of plant abnormalities.

I. FASCIATION.

This is a common phenomenon, and so widely distributed that it has been observed by all who have come into any considerable contact with plants. The present cases are described here because of certain interesting attendant characters which may throw some light upon the nature of fasciation.

A remarkable case of fasciation was observed in *Leptilon* (*Erigeron*) *Canadense* L., where a stem had a breadth, in the dried state, of 8.5^{cm}, and the overgrowth at the crest was so great as to throw it into marked undulations. The margins of this stem were apparently normal, as were also the leaves borne on them ; and one margin gave rise to a series of normal axillary branches. On the broad sides of the stem, however, the leaves were reduced to a narrowly linear form 0.5–2^{mm} by 2–4^{cm}. This reduction was probably correlated with two other conditions, (1) the great crowding of the leaves, and (2) the greatly increased surface of the stem compared with its volume. It is certain that photosynthesis was carried on chiefly in the tissues of the stem itself, which had an unusually bright green color and delicate texture. No buds were produced in the axils of these reduced leaves until within 6–8^{cm} of the crest, above which point each axil produced a sessile flower bud. The whole side of the stem was covered with numerous fine ridges which, on being traced to their origin, were found to originate in the midribs of the leaves. According to Masters[3] "the striae which these stems almost invariably present exhibit the lines of junction" between the stems by whose union the fasciated stem is formed; but this certainly cannot be true of the striae in this case.

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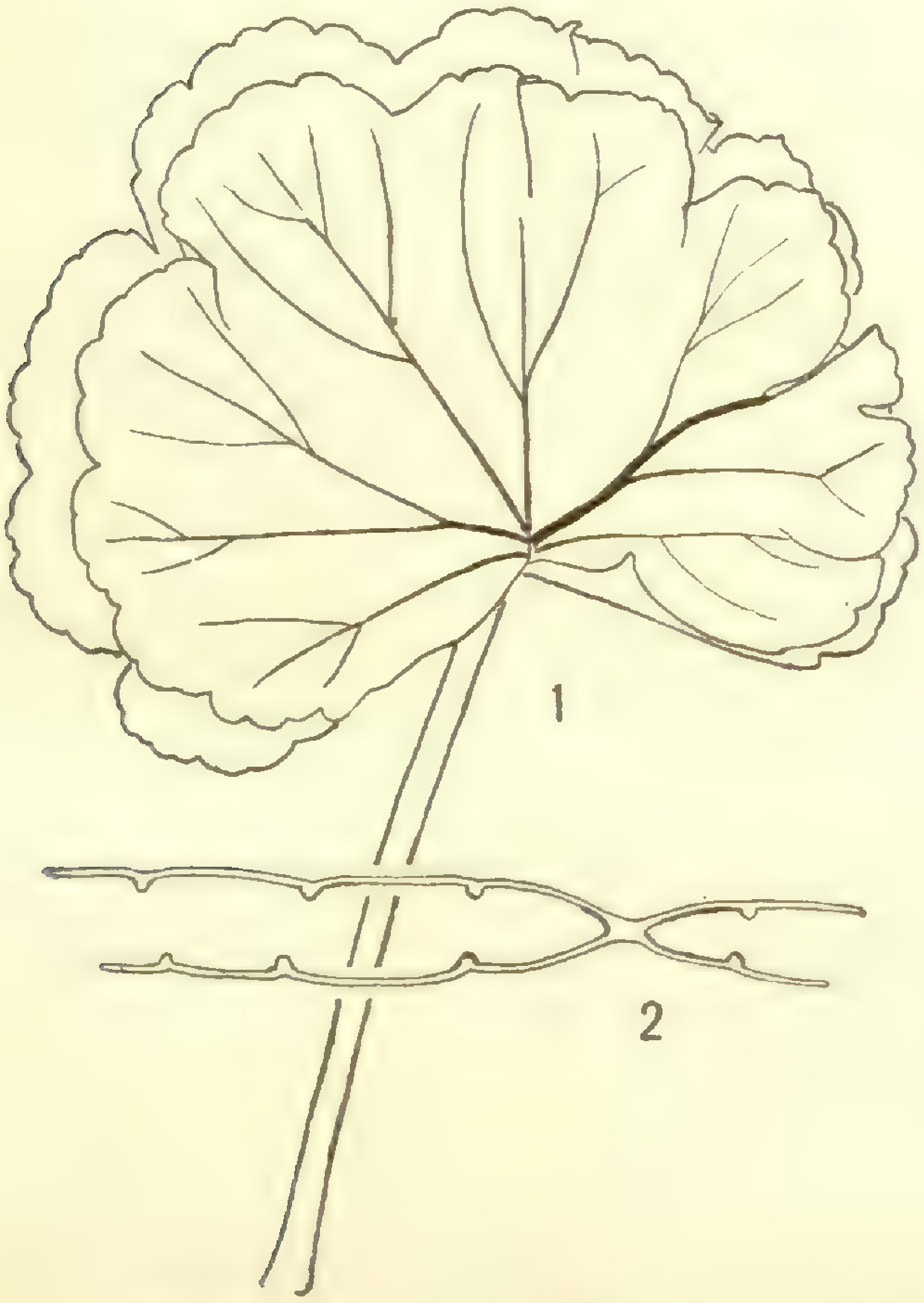
[1] Contributions from the Biological Laboratory of Antioch College. No. 3.

[2] O. PENZIG, Pflanzen-teratologie. 2 vols. Genoa.



FIGS. 1, 2.—*1*, Leaf of *Pelargonium* sp. with two blades. *2*, Cross section through blades of leaf shown in *fig. 1*, showing the reflection.

In a fasciated stem of *Echium vulgare* L. there was found a greater width near the ground than at a point just below the widening at the crest. Here too the striae are simply the grooves between ridges, which are all plainly traceable to the midribs of the leaves and are undoubtedly the lines beneath which lie the fibrovascular bundles originating in the leaves. By offering a different explanation of these striae the evidence of the union of stems in fasciation is lessened by so much, though not destroyed, since a union may exist without the existence of an evident line of union.

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[3] Vegetable Teratology 16. London, 1869.

II. ABNORMAL FOLIAGE LEAVES.

One of the most common abnormalities in Pelargonium is the formation of peltate and funnel-shaped leaves by the growth of leaf tissue where there is normally a sinus. On a specimen which had been observed to produce a number of peltate leaves, there was also found the exceedingly interesting form shown in *figs. 1* and *2*. The petiole was about 1.5 times as broad as a normal petiole and bore two perfectly formed blades. These blades were united from base to margin along a single vein and were placed with the under sides opposed to each other. This leaf gives an excellent illustration of Bateson's[4] (1894) law of reflection, *i. e.*, in the duplication of an organ the arrangement of the parts is the reverse of the arrangement of homologous parts in the normal organ. So perfect was the reflection in this case that the more minute details of outline were reproduced almost as perfectly as in a mirror.

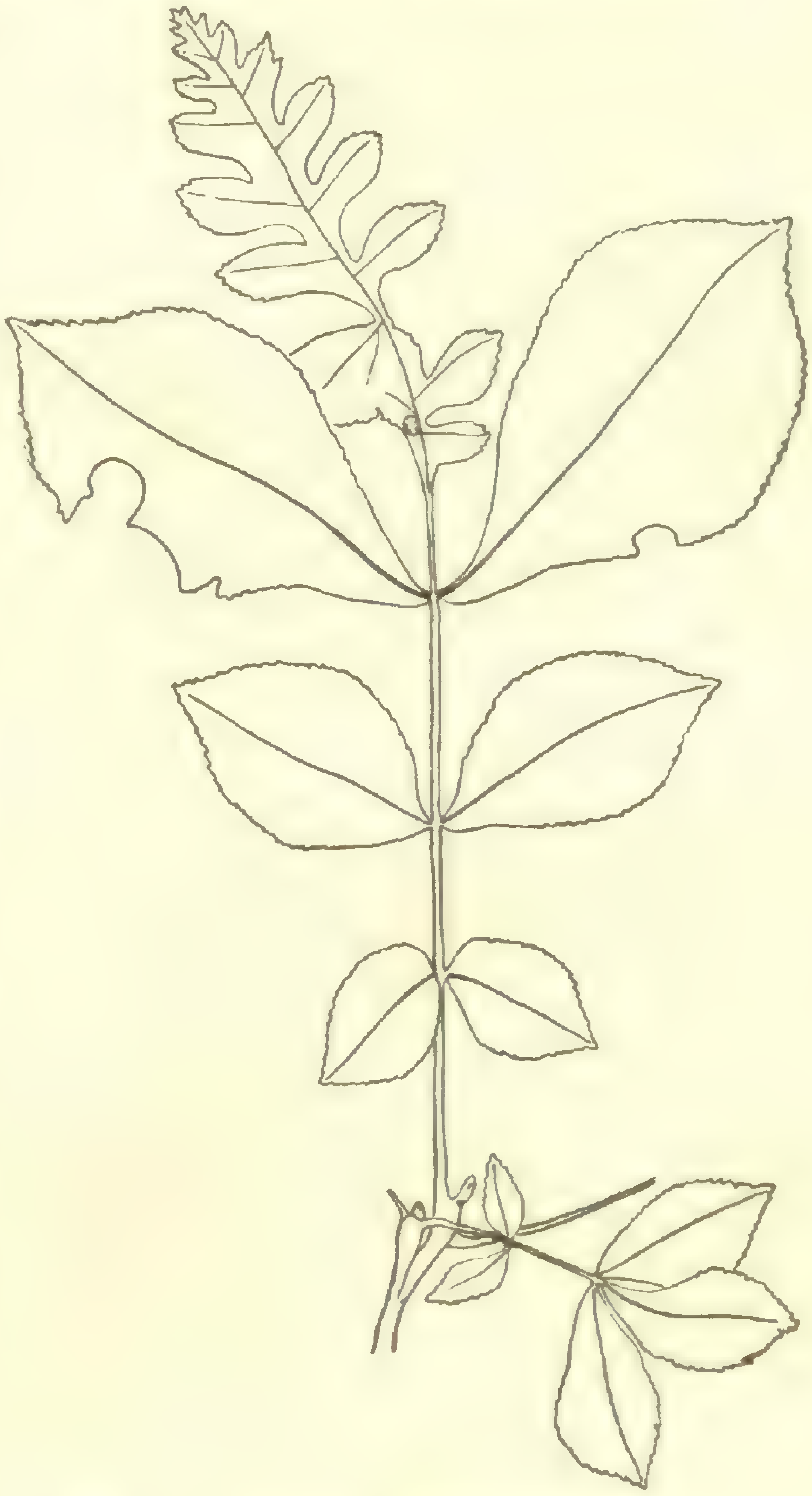

FIG. 3.—Leaf of Hicoria sp. showing a deeply lobed terminal leaflet.

In a leaf of *Hicoria* sp. (*fig. 3*), collected several years ago by the writer, the terminal leaflet was so regularly and deeply lobed as to be almost compound. This modification was decidedly "progressive," although it occurred in the terminal leaflet, where, as has been so well pointed out by Jackson[5] (1899) the most primitive form is to be expected. There was a small gall just at the base of the leaflet, and as it lay close to the midrib and partially deranged its tissues, the peculiar form of this leaflet may have been due to a pathological condition.

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[4] W. BATESON, Material for the study of variation, 474–575. London and New York.

III. ABNORMAL FLORAL ORGANS.

In the summer of 1900 a small plot of *Lathyrus odoratus* L. was found to be producing a considerable number of abnormal flowers. A few of these were dissected and the parts carefully drawn at the time (*figs. 4–30*). The inflorescence of this species usually has only three flowers, but occasionally varies from two to four. *Fig. 4* represents a double inflorescence in which a two-flowered inflorescence has apparently arisen, axillary to the lower flower of a four-flowered inflorescence. Abnormal floral organs were numerous and interesting. I have shown the parts and arrangement of the normal flower in *figs. 5–7*. The combination of abnormalities in each flower can best be exhibited by description of the cases examined. In each case the floral organs not mentioned were normal.

Case 1. An outgrowth from the margin of the sinus between the upper calyx teeth assumed the form and coloring of the vexillum. Vexilla two. (*Fig. 8.*)

Case 2. Calyx with a petaloid outgrowth from the upper sinus. This outgrowth had a lanceolate form instead of the nearly orbicular form of the vexillum. Vexilla two. Stamens eleven, all united.

Case 3. The upper edge of an upper calyx lobe dilated slightly and colored. Vexilla two, the outer having a downward hook like that of an ala, and somewhat narrower than normal. Stamens eleven, two nearly free at the base but united to the other nine above. (*Fig. 9.*)

Case 4. Calyx the same as in *1*. Vexilla two. Stamens twelve, all united to form a tube.

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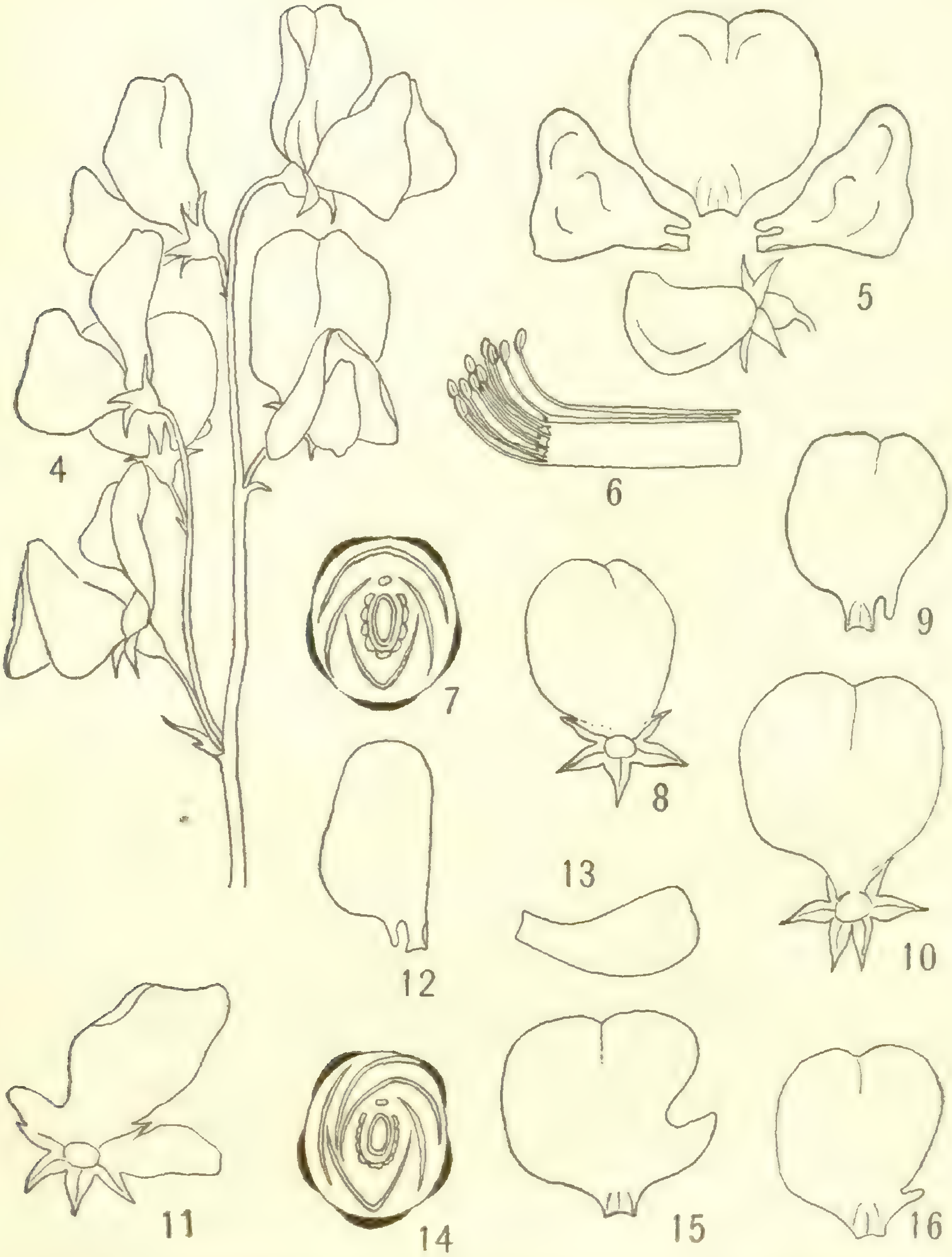
[5] R. T. JACKSON, Localized stages of development in plants and animals. Mem. Boston Soc. Nat. Hist. **5**: 89–153. *pls. 16–25.*



FIGS. 4–16.—Abnormal floral organs in *Lathyrus odoratus*. For details see text.

Case 5. Calyx normal in form but with a touch of color between the upper teeth. Vexilla two, the inner one having one margin enclosed within the carina.

Case 6. Calyx with six teeth, and with a large expansion between the upper ones. One margin of this expansion was free and inserted within the calyx like a vexillum. This structure was probably a union of a vexillum with a petaloid outgrowth of the calyx, although no line of junction was apparent. Free vexillum none. Stamens ten, united into a split tube. (*Fig. 10.*)

Case 7. Calyx as in *1.* Vexilla two, one with a downward hook. Stamens eleven, united into a tube.

Case 8. Calyx as in *1.* Rest of flower normal.

Case 9. The tissue of two of the upper sinuses of the calyx was expanded into irregular petaloid bodies, the upper one with a divergent lateral lobe. Vexilla two, each having the form of half a normal vexillum, one with a prominent downward hook. Alae abnormally narrow, curved upward and outward, and lacking the usual overlapping edge. Stamens twelve, of which eleven were completely united, the twelfth partially adherent. (*Figs. 11–13.*)

Case 10. Calyx with a slight petaloid expansion which was united edge to edge with the outer vexillum. Vexilla two, each having one margin enclosed in the carina. One ala external. (*Fig. 14.*)

Case 11. Calyx the same as in *1.* Vexilla two. One ala narrow and much curved upward. Stamens nine united, one free, and one nearly free.

Case 12. Calyx with six teeth. Vexilla two, each with a lateral lobe, one lobe unusually large. (*Fig. 15.*)

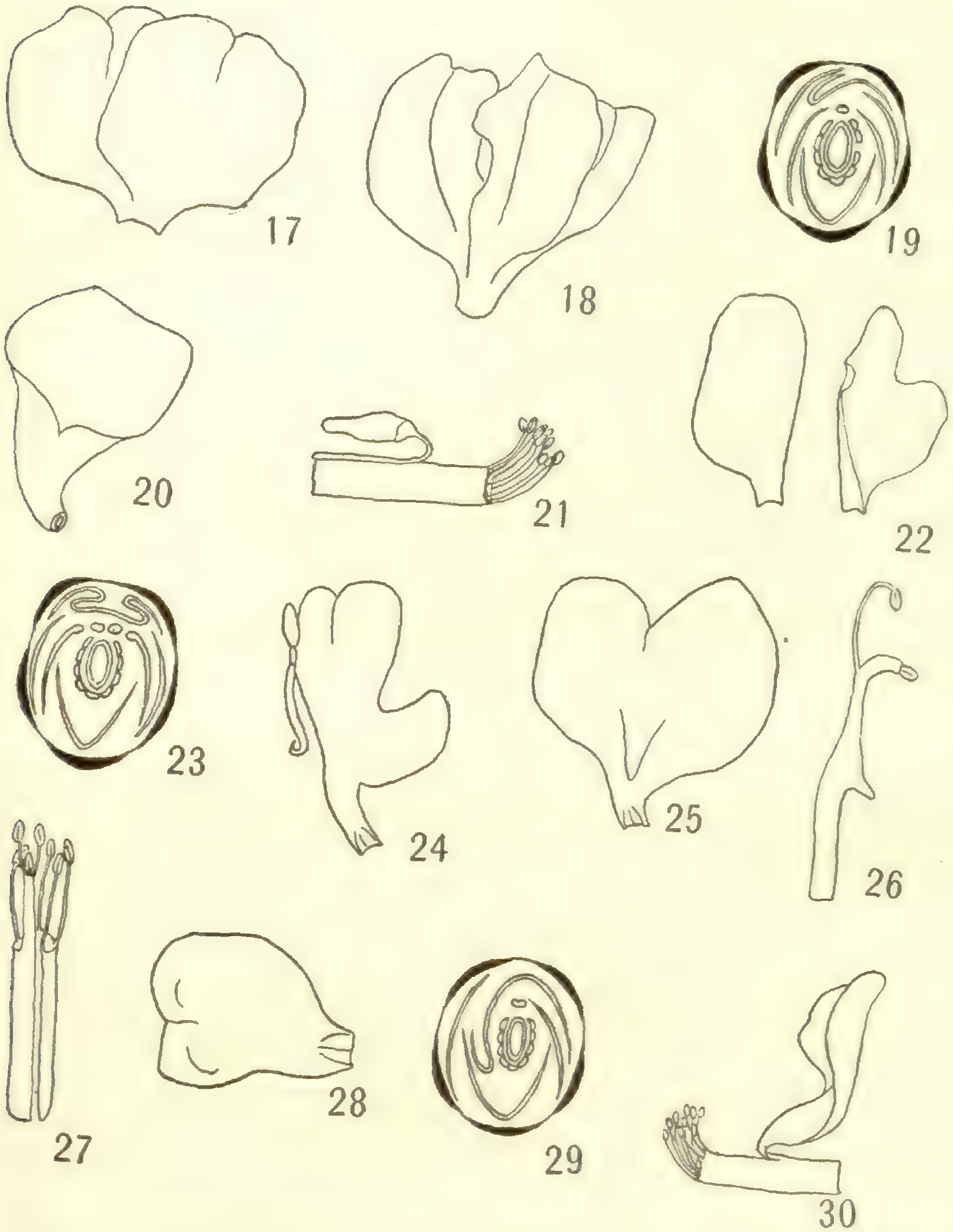
Case 13. Calyx teeth six, the lower two narrower and more approximate than the others. Vexilla two. Stamens nine united, three free.

Case 14. Vexilla two. Stamens nine united, and two free.

Case 15. Vexilla two, each with a lateral basal lobe on the upper side. (*Fig. 16.*)

Cases 16 and *17.* Vexilla two, the second having one margin enclosed in the carina. Stamens ten united, one free.

Case 18. Vexilla two, which were slightly united edge to edge at the base. Stamens diadelphous, two and nine. (*Fig. 17.*)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Figs. 17–30.—Abnormal floral organs in *Lathyrus odoratus*. For details see text.

Case 19. Vexilla three, all alike and nearly normal in form.

Case 20. Vexilla three, all united. Stamens nine united, three free. (*Fig. 18.*)

Case 21. Vexilla three, the middle one with one side folded back upon itself. Stamens triadelphous, one, two, and seven. (*Fig. 19.*)

Case 22. Vexillum with margins turned backward and coalesced, forming a funnel which was adherent to the calyx tube at the base. Stamens two free, nine normally united, with a twelfth united for two-thirds of its length. This filament was slightly enlarged and colored, and had its anther converted into a body of the same color and texture as the petals. (*Figs. 20, 21.*)

Case 23. Vexilla two, the second shaped like half the first and balanced on the other side by a petaloid stamen having a yellow spot, corresponding to an anther, on the inner margin. Other stamens normal, nine united and one free, the free stamen arising between the two petaloid bodies within the normal vexillum. (*Fig. 22.*)

Case 24. Vexillum doubled upon itself on both sides. Alae two on each side, the supernumerary alae having the hooks on the lower side, *i. e.*, toward the normal alae, in this respect appearing as a reflection of them. One of these supernumerary alae occupied the position of a free stamen. Stamens nine united, two free. (*Fig. 23.*)

Case 25. Vexilla two, the first notched to one side of the center, the second with a large lateral lobe, and having one margin enclosed in the carina. The enclosed margin of the second vexillum bore a small appendage which was nearly spiral below and ended above in an erect wing. This appendage was probably the homologue of an anther. (*Fig. 24.*)

Case 26. Vexilla two, the outer joined below, margin to margin, with one ala.

Case 27. One ala joined to the first vexillum, this double petal external. Second vexillum of normal form, but with one margin included in the carina. Upper stamen free (as normal), beside it a broad filament with a lateral overlapping hook and colored like a petal. This broad filament was topped with an anther and had a normal filament branching from it at a point two-thirds of its length from the base. The remaining stamens were united into a split tube bearing upon its outer margin four normal filaments, and one broader filament formed by the union of three filaments. This bore at its summit one sessile anther, and at each side of this sessile anther a short-stalked one. (*Figs. 25–27.*)

Case 28. One ala external and lacking the usual hook. One side of the vexillum folded back and included in the carina. (*Figs. 28, 29.*)

Case 29. Nine stamens united, the tenth united to the other nine for half the length of the tube, then spreading back with the form and coloring of a second vexillum. (*Fig. 30.*)

These abnormalities may be summarized as follows:

1. Abnormalities of the calyx. (*a*) In two cases there were found six calyx teeth, and (*b*) in eleven cases a petaloid inflation grew from the sinus between the upper teeth. This petaloid outgrowth varied from a small colored area in a normally formed sinus to an expanse of tissue having the size, form, and color of a perfect vexillum.

2. Abnormalities of the vexillum. (*a*) In twenty instances there were two vexilla, and in three cases three vexilla were found. In about half, the second vexillum was normal in form, the variations from this being in two directions, (i) toward the wing with its downward hook on the one hand, and (ii) toward the stamen on the other. (*b*) In two cases there was a union between an ala and the outer vexillum. (*c*) Union of the vexilla was found in two instances.

3. Abnormalities of the alae. (*a*) In two flowers the alae were unusually narrow and curved upward. (*b*) In two cases, as mentioned above, there was a union between an ala and a vexillum. (*c*) In one case there were two alae on each side.

4. Abnormalities of the stamens. (*a*) An approach to the form and coloring of the petals. Almost every degree of petalody was found from a petaloid appendage or a broadened filament with a hook, to the form of half a vexillum. (*b*) Three flowers had two free stamens, and two had three free stamens. (*c*) Thirteen had an unusual number of united stamens, mostly ten or eleven, in two instances reaching twelve. (*d*) In several

the stamens were triadelphous, one, two, and nine, or one, two, and seven.

5. Abnormal aestivation. (*a*) In three cases one ala was external to the vexillum. (*b*) In six instances the supernumerary vexillum had one margin enclosed within the carina. (*c*) In several cases there was an abnormal folding of the vexillum upon itself.

There have been but few cases recorded of the union of sepals in *Clematis*, and belonging as it does to a family which typically has all the parts distinct, the union of parts is all the more remarkable. Perhaps the most noteworthy case of this kind is that described by Jaeger[6] (1828), in which the sepals of *Clematis Viticella* L. were united into a bilabiate tubular perianth. Ch. Fermond[7] (1884) has found many cases of three-parted perianths in *Clematis* sp., and Cockerell[8] (1897) remarks upon the common occurrence of the union of two sepals in *C. ligusticifolia.* In a specimen of Clematis growing at Edgewood, North Hampton, O., said to be a seedling of *C. Jackmani* of the gardeners, there are found every year many cases of similar union of sepals, and in varying degrees of union, from the slight union of two sepals to the complete union of all the sepals into a regular, tubular, gamosepalous flower (*figs. 31–34*). This complete union, shown in *fig. 34*, does not occur often, but I have found two like the one figured. If this is a seedling of *C. Jackmani*, its variations are rather remarkable because of the almost absolute invariability of that form. In the "Star of India"[9] Clematis there is a marked tendency to depart from the typical four-parted perianth, and to produce flowers having six sepals. In this species are found many cases of division or of union of sepals.

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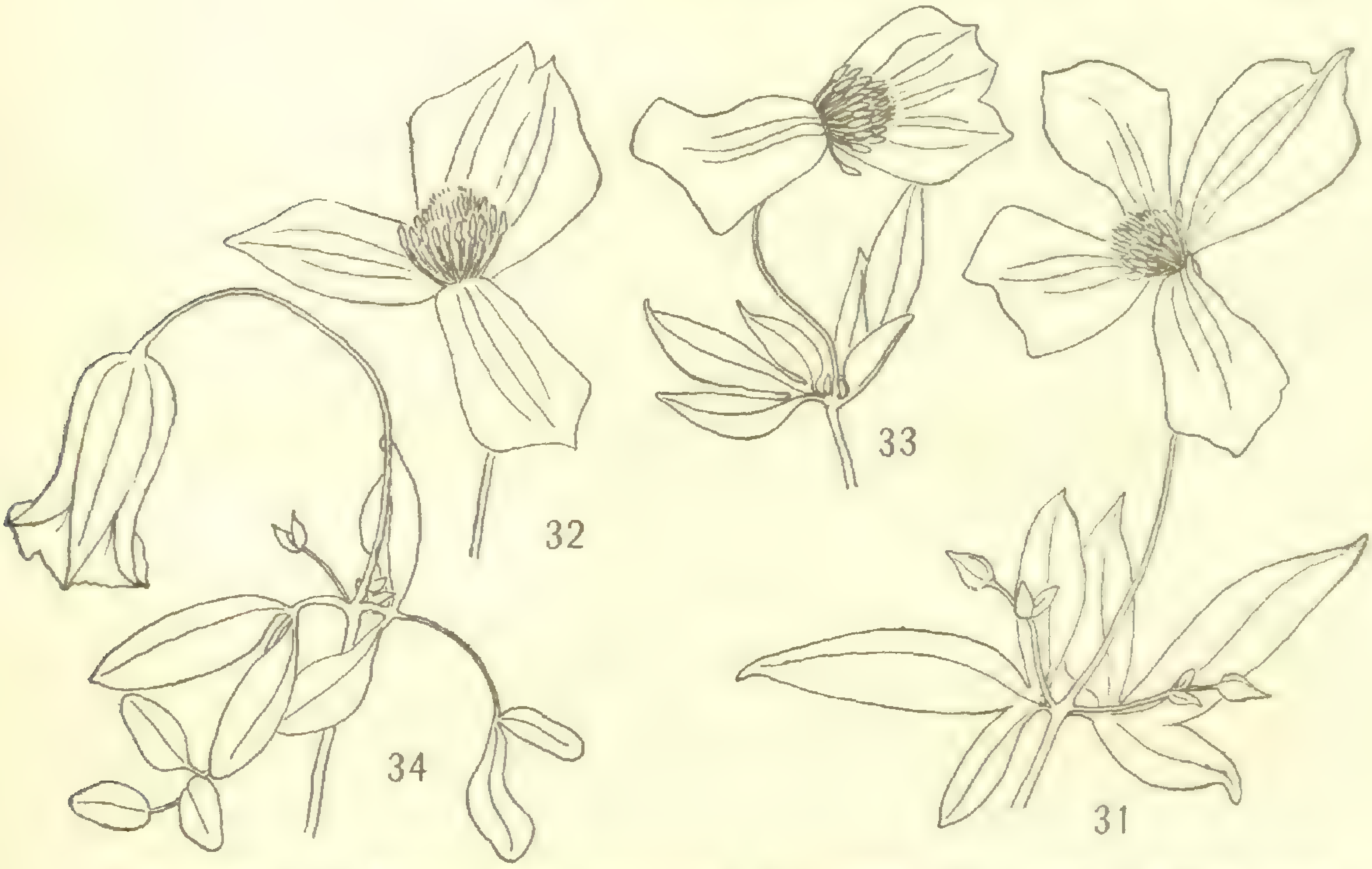
[6] Nov. Act. Acad. Caes. Leop. **1828**: 641. *pl. 37.*

[7] Essai de phytomorphie, ou étude des causes qui déterminent les principales formes végétales. 2 vols. Paris.

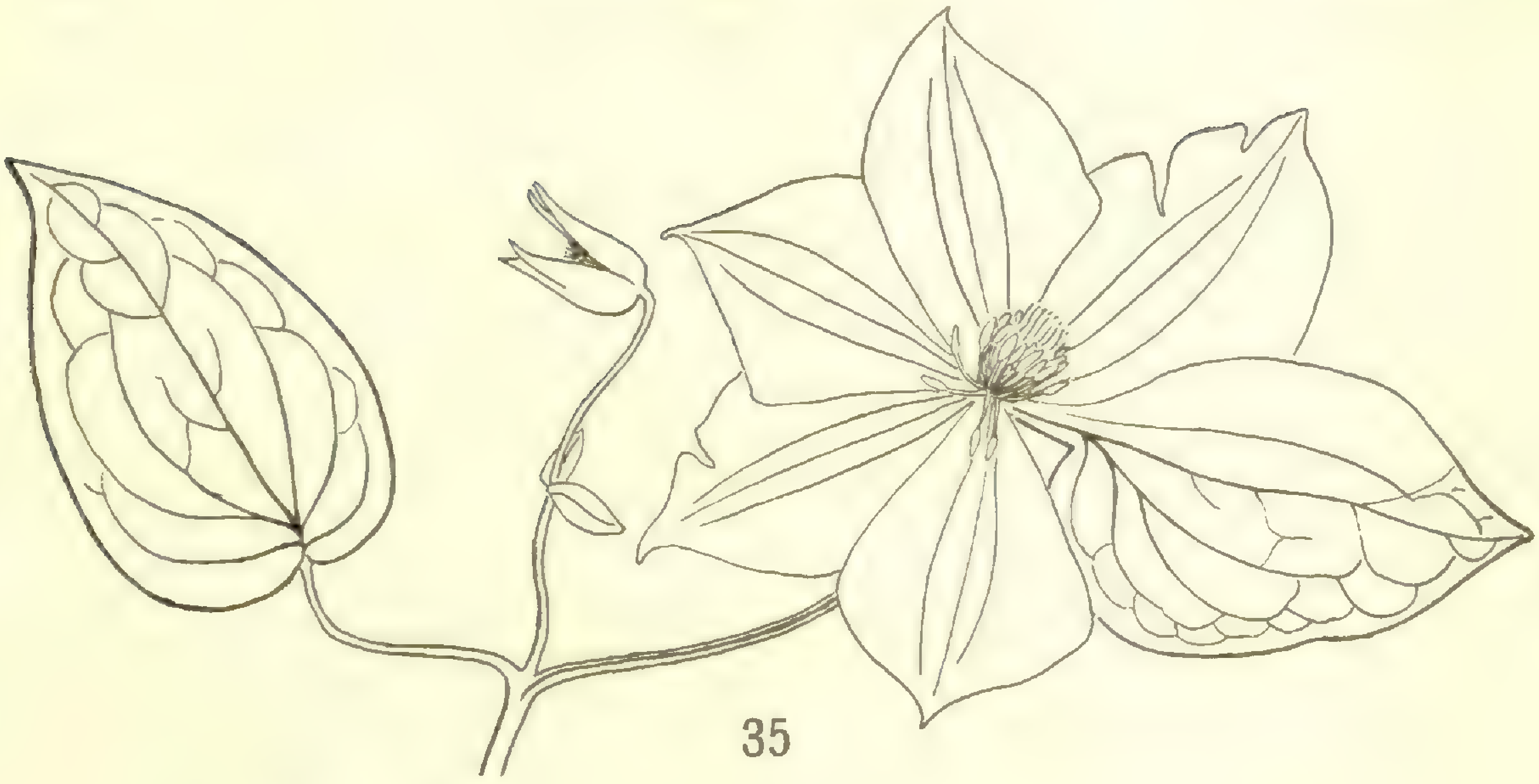
[8] BOT. GAZ. **24**: 293.

[9] This is the garden name. I have been unable to determine its specific relationship.

Two of the most striking cases of abnormality in Clematis are shown in *figs. 35* and *36*, although similar cases have been frequently described, indicating that the displacement and coloring of the leaves which are nearest the flowers is a common abnormality in the genus. The two figured were both collected from the same plant of the "Star of India" Clematis, although several seasons intervened between them. In *fig. 35* there appears what at first seemed to be a reversion of the greater part of a sepal to an ordinary foliage leaf; the remainder retained the form, delicate texture, and rich coloring characteristic of the sepals. On the examination of the normal inflorescence, however, it appears that this organ, instead of being a partly reverted sepal, in reality is the result of a coalescence of a sepal and a leaf from the node next below the flower. The chief evidences of this are found in the absence of one of the leaves from that node, and the presence of a marked decurrent line extending from the leafy organ down the side of the peduncle to the node.



FIGS. 31–34.—Abnormal floral organs in a seedling of *Clematis Jackmani* (of gardeners); **31, normal flower; 32, two sepals united; 33, three sepals united; 34, all the sepals united into a gamosepalous perianth.**



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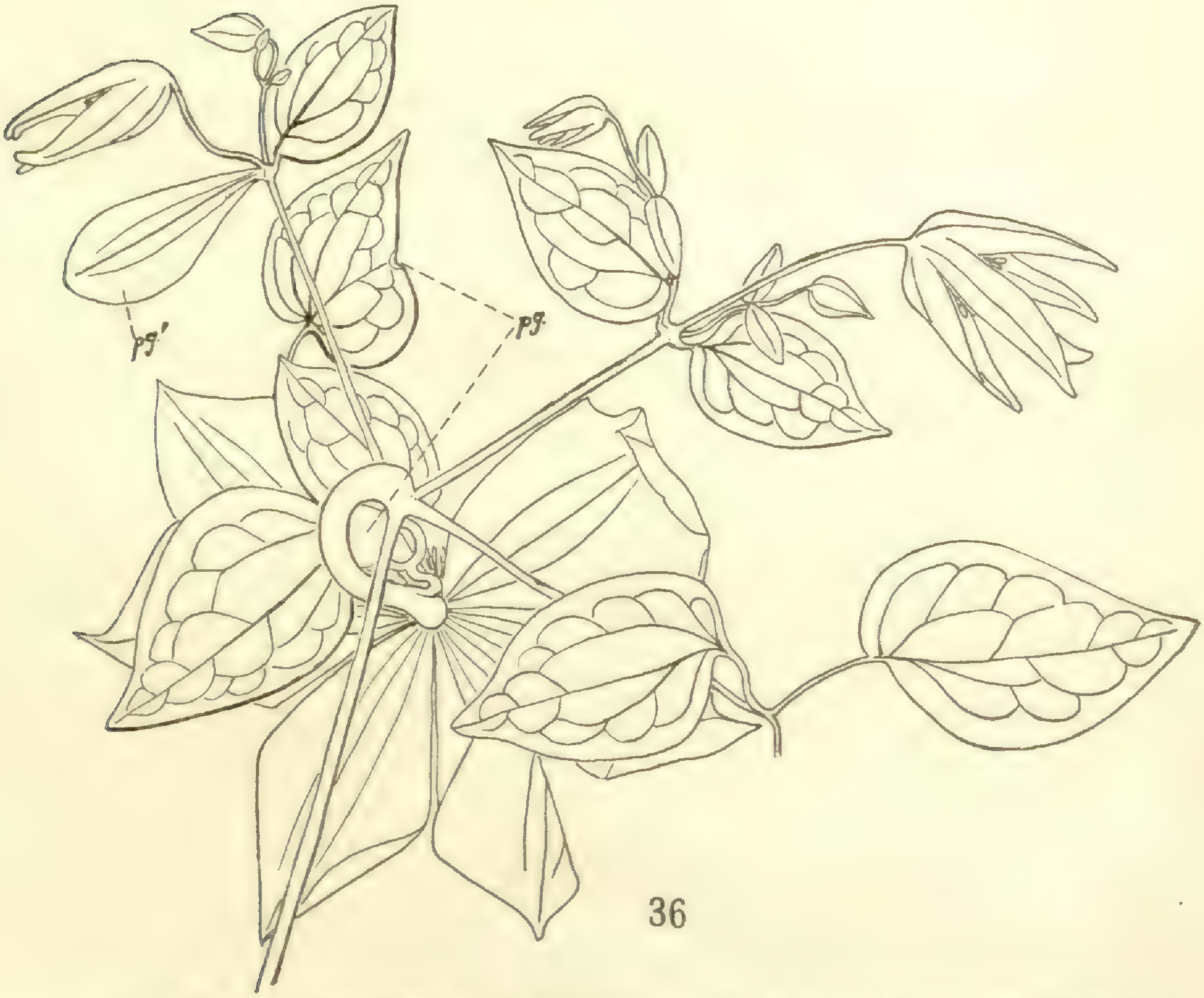

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FIGS. 35, 36.—Abnormal floral organs in "Star of India" Clematis (of gardeners); *35*, union of leaf and sepal; *36*, union of peduncle and petiole, one leaf with leaflets partly colored (*pg*), and one leaf entirely changed to a sepaloid body (*pg'*).

The bud which is normally axillary to the removed leaf failed to develop.

Fig. 36 is a somewhat similar case, but more complicated. Here, too, there is an adnation of the petiole of the leaf to the peduncle, and two of the three leaflets are partly colored like sepals. From the groove at the side of the coalesced petiole and peduncle arises an axillary branch. This branch bears, at the next node above, a leaf which in every respect resembles a sepal, and which failed to produce a bud in its axil.

All the cases here described and figured are in the herbarium of the writer, except those of Lathyrus which were dissected, and the parts sketched and described from the fresh material.

YELLOW SPRINGS, O.

BRIEFER ARTICLES.

MEISSNER ON EVERGREEN NEEDLES.

(WITH ONE FIGURE)

A RECENT double number of the *Botanische Zeitung*[1] is devoted to a third treatise by Meissner on evergreen needles. This time the theme is chiefly the relation of the length of stem and needle, in support of his previous attack on the idea advanced by Kraus,[2] and supported by myself,[3] that the thrifty growth of stem and leaf may be expected to occur together. Part I of Meissner's paper contains in tabulated form numerous measurements of stems and needles of Pinus, Abies, and Picea. In a large part of these the variations in needle length are without any apparent relation to that of the stem. Negative testimony of this kind is not very strong, for a more judicious than judicial selection of material can make it show almost anything. For instance, Meissner (p. 30 *et seq.*) would prove by it that I am unreasonable in expecting the different parts of one tree to vary alike in the growth of stems and needles.[4] While it must be said that the frequency of exceptions has surprised me, it has still seemed to me in the observation and measurement of conifers, wild and cultivated, in various parts of the United States, that in a great majority of instances the stems and needles vary in length together. But perhaps Meissner would have drawn the opposite conclusion in the same forests, with an equal desire to see things as they are. Results obtained by the statistical method can hardly ever have the weight of those yielded by judicious experimentation.

Part II deals with mutilation experiments. As would be expected, if the mutilation compels the tree to devote its plastic material to the development of a few members, their growth will be stimulated: while robbing it of plastic material or the chance to form, it results in a stunted growth.

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[1] Ueber das Verhältniss von Stamm- und Nadellänge bei einigen Coniferen. Bot. Zeit. **59**: 25. 1901.

[2] Abhandl. d. naturf. Gesells. zu Halle **16**: 363. 1886.

[3] A biological note on the size of evergreen needles. Bot. Gaz. **25**: 427. 1898

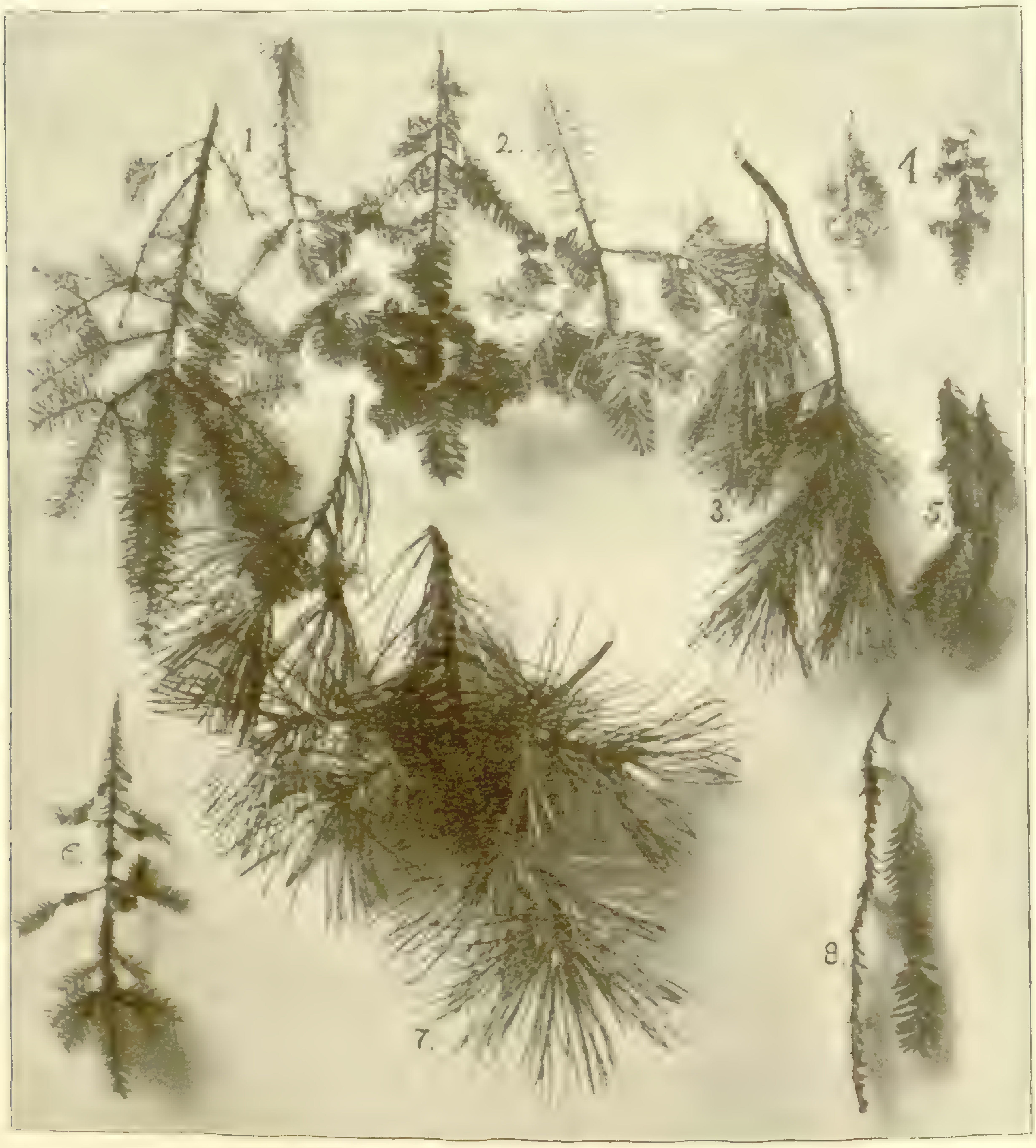
[4] The proportionate length of stem and needle on the main axis and its branches *in one season* is an altogether different subject.

Part III, on the annual period of growth of stems and leaves, is the most valuable part of the paper. Meissner shows by measurements that the chief growths in length of stems and needles fall at different times. In Pinus the stem almost finishes its season's elongation, while the needles remain relatively short, the relations in Abies and Picea being just the reverse of this. The dry weights of stems and needles at various times during the months of growth vary in general with the lengths. A moment's reflection will satisfy anybody who has seen evergreens grow that Meissner is correct. Transitory unfavorable conditions early in the season will therefore tend to hinder the growth of the stem of Pinus more than that of the leaves. The maximum growths of stems and needles at different times is a physiological explanation of the cases in which short year's-stems bear long needles, or *vice versa.* But while this makes exceptions intelligible, I am by no means ready to agree that there is no connection between the sizes of stems and needles, or that Kraus and I were wrong in expecting both to vary, in nature, with the general condition of the plant. Neither of us could have thought of maintaining that leaves and stems could never vary independently; that external factors, such as light, must directly influence both alike. Trees do not respond at once to changes in the weather to such an extent that they will often be stunted in May and thrive in June, or grow luxuriantly in May and then abruptly halt. At least my observations on the whole resultant growth indicate that they do not.

The influence of bad conditions on the stages of growth previous to active enlargement has been left largely out of account, and may appropriately receive a word here in the light of Meissner's results. In my paper the area of cross sections of the needles was given, and was always least the season following transplanting. The difference was due to the size of the cells, the number not being materially different from that of other years. Thus in leaves of *Pinus Austriaca* (cf. *loc. cit.* p. 433) the number of cells in cross section was as follows:

	1895	1896	1897
Epidermis	176	176	246
Outer parenchyma layer	77	76	96
Endodermis	39	38	48

The number of cells was surprisingly the same in 1895 and 1896, though the difference in size was very great. The leaves of 1897 were exceptionally thrifty in all respects. The larger leaves contained more resin ducts. This plant was transplanted rather late, when the leaves of deciduous trees were beginning to grow, probably about the first of April. The exact date is not known, and is not important because it would indicate a definite stage in development only for the one year and locality. The fact that the trees did not have their growth checked



CONCOMITANT DWARFING OF STEMS AND LEAVES OF CONIFERS.

1. Picea alba; 2. Abies balsamea; 3. Pinus Strobus; 4. Tsuga Canadensis; 5. Picea pungens; 6. Picea nigra; 7. Pinus Austriaca; 8. Taxus baccata.

before the first phase of the season's growth is indicated not only by the full number of cells, but also by the presence usually of at least the normal number of needles (*loc. cit.* p. 429).

There are a number of trees of *Picea excelsa* on the campus of West Virginia University that were transplanted in 1899, several weeks earlier in the season than the Bloomington trees. While the size of the cells is not nearly proportional to that of the needles, the number formed during the spring following transplanting falls somewhat behind. The numbers in an average case are as follows:

	1898	1899	1900
Epidermis	122	114	140
Outer parenchyma layer	91	80	106
Endodermis	22	18	25

The whole question of the growth of the needle will reward more experimental study, and Meissner's interesting paper should stimulate it.

The accompanying photograph is of the plants described by me in 1898, and will show the concomitant dwarfing of stems and needles better perhaps than tables of measurements did.—Edwin Bingham Copeland, *Monroe, Wis.*

THE INSTABILITY OF THE ROCHESTER NOMENCLATURE.

Since the publication of my article in the Botanical Gazette for last March[1] three communications have appeared which discuss certain details there presented. Two of these letters, from Mr. C. L. Pollard[2] and from Professor L. M. Underwood,[3] question the significance of facts presented by me in parallel columns; while a third letter, from Professor N. L. Britton,[4] presents at more length than was done by me the practical reasons why the first species of a complex genus should not necessarily be treated as the type. These articles bearing directly upon the vital question of stability in botanical nomenclature must leave the general reader in some doubt as to the exact force of certain arguments I have already discussed. It may not be out of place, therefore, to ask for a brief consideration of the points thus newly emphasized.

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[1] Bot. Gaz. 31:183. 1901.

[2] *Ibid.* 31:285. 1901.

[3] *Ibid.* 31:365. 1901.

[4] Science 13:588. 1901.

Mr. Pollard quotes from my article certain sentences embodying conclusions which he characterizes as misleading. The conclusions thus referred to were to the effect that in 1900 Professor Underwood, following logically and consistently the Rochester Code, used 25 per cent. of names different from those used by him in 1896, when he likewise asserted that he was following the Rochester Code. Mr. Pollard's contention is that this fact does not afford a proper basis for criticism of the Rochester Code, because most of the changes made by Professor Underwood represent very recent segregations among the ferns, comparable with the divisions made within three years in the genus Antennaria. Yet it does not seem to have occurred to Mr. Pollard that, in omitting the footnote to the paragraph quoted, he is possibly misleading that large body of readers who habitually neglect to verify quotations and references. Had he carefully read and quoted the two sentences as they were originally published with the footnote: "The true ferns alone are here considered, and the genus *Botrychium* is purposely omitted, since that genus has been subdivided by Professor Underwood to such an extent that comparative figures would have little definite significance," he would have found it unnecessary to inquire whether I do not "recognize the necessity for occasional segregations." Every working systematist must recognize such necessity; but the segregation of perplexing polymorphous types is a very different thing from the raking up of older and more or less obscure appellations for plants the names of which have long been established. The latter is a nomenclatorial matter, the former botanical; and if anyone has read into my previous remarks the least opposition to such division of confused groups as shall lead to a clearer understanding of the forms, he has found that which I in no way intended.

But most of the ferns under discussion cannot be placed by Mr. Pollard under the same category as the recent segregates of Antennaria (and likewise Botrychium), for *they do not represent new points of view unknown in 1896*. Matteuccia is a name given in 1866 to Willdenow's Struthiopteris, which was segregated in 1809 from Osmunda; our Dennstaedtia was separated from Dicksonia in 1857; Filix was published by Adanson in his well known *Famille des Plantes* in 1763; Phyllitis was re-distinguished in 1844; and it is certainly not a new idea to treat species of the complex genus Aspidium under the name *Polystichum*. Neither are *Phegopteris Robertiana* and *Notholaena dealbata* now treated as species for the first time. The former was published by Hoffmann in 1795 as *Polypodium Robertianum*, the latter by Pursh in 1814 as *Cheilanthes dealbata*. In 1896 Professor Underwood had already published five editions of a work on North American ferns, and he was consequently in a position to know of the earlier conceptions and treatments of these plants. At that time he was publishing according to his interpretation of the Rochester Code, and the names thus published, we were assured, were those which would stand. Yet after having established (as he supposed) these names according to strict priority principles he has found occasion to alter 25 per cent. of them. Has his application of the Rochester Code brought uniformity?

In his "Open Letter" Professor Underwood shows very conclusively that "when its bald statements are unqualified," "the deadly parallel" "seems to mean more than the facts will warrant." For, avowedly with the purpose of showing that "the personal preference hit-or-miss system of Kew and Berlin" is bringing us unwarranted confusion in plant names, he places in parallel columns twenty-one fern names which appeared in the *first* edition of Gray's *Manual* and the twenty-one more or less dissimilar names for the same plants in the *sixth* edition. By the thoughtless reader, with "its bald statements . . . . unqualified," this comparison might seem completely to dispose of my criticism of the recent changes of names made by Professor Underwood. Yet it should be borne in mind that such comparisons may "mean more than the facts will warrant." Professor Underwood implies that the application of the combined Berlin and Kew rules is responsible for the changes between the first and the sixth editions of the *Manual*. Can it be that he "forgot" that the *first* edition was issued in 1848, the *fifth* edition (Pteridophyta by D. C. Eaton) in May, 1867, and the *sixth* edition in 1889, *all before the Berlin rules were formulated in 1897?*

It was three months after the fifth edition of the *Manual* went to press that the Paris convention of 1867 was held and the DeCandollean Code was drawn up. Consequently the sixth edition (1889), by Watson and Coulter, was the only one published after the adoption of the Paris Code of 1867. Furthermore, since even this edition was published eight years before the rules of the Berlin botanists, a comparison of the first edition (1848) and this sixth edition (1889) is no very logical proof that the Berlin rule of 1897 is "unseaworthy."

The fact is, that the names in no edition of Gray's *Manual* have been based on the combination of the Berlin rule for genera and the so-called Kew rule for species, which was recently advocated by me.

This simple and definite method of obtaining a uniform system of names has been carefully tested, however, during the past half decade, and it has appealed as practical to many besides the "trans-Carlines."

Let us now consider, on the other hand, the points raised by Professor Britton. The first rule of the Rochester Code reads: "Priority of publication is to be regarded as the fundamental principle of botanical nomenclature." The fifth rule that "*Publication of a genus consists* only (1) in the distribution of a printed description of the genus named; (2) *in the publication of the name of the genus and the citation of one* or more *previously published species* as examples or types of the genus, with or without a diagnosis" [italics ours]. A recommendation adopted by the reformers at Madison reads: "In determining the name of a genus or species to which two or more names have been given by an author in the same volume or on the same page of a volume precedence shall decide."

By Professor Underwood, as already emphasized in the March GAZETTE, this principle of strict priority has been applied in the determination of the type of a complex genus. Professor E. L. Greene, likewise, has made important changes based upon its rigid enforcement. Professor Britton, too, has more than once maintained that priority of place (precedence) is final, saying, in regard to the now famous case of Buda and Tissa: "I accepted *Tissa* rather than *Buda* for the simple reason that it *stands first on the page* in Adanson's 'Familles.' *That is priority, I am sure*" [italics ours].[5] He has further said that this principle (priority of position) will be accepted by those "who have recognized the necessity of adopting methods of procedure which will render the system of nomenclature stable."[6] And again, "the number of cases in which change is desirable by reason of priority of place is not great."[7] Thus, in 1890, Professor Britton clearly defined what he meant by priority. In 1892, "after a very careful consideration," the Rochester Code was formulated; and in 1893, after plenty of time for further deliberation on its fundamental principle, the code was augmented by the recommendation above quoted.

Priority has been talked of until the subject has become a tedious one; and that it is the ruling principle of the reformers has been so often avowed as to become axiomatic. It is not surprising, then, to find, in the *Illustrated Flora* in 1896, the statement that "its [priority's] adoption is the only practicable way of securing stability to the original names." This idea has permeated the writings of the reformers, and they have over and over again asserted in books and papers for amateurs and "the younger generation" that the names they advocate are alone the ones which can stand.

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[5] Jour. Bot. **28**: 295. 1890.

[6] Jour. Bot. **28**: 371. 1890.

[7] Jour. Bot. **28**: 372. 1890.

That the principle of strict priority (the fundamental law of the Rochester Code) has been many times ignored by those who claim to follow it was sufficiently emphasized in the March GAZETTE. Indeed, when Professor Greene pointed out,[8] in 1896, that the principle of priority demanded that the first species of a complex genus be taken as the type, he was merely showing the logical outcome of the principle. When again, in 1899, Professor Underwood followed the same interpretation in his *Review of the Genera of Ferns*,[9] he was merely following conscientiously the fundamental principle of the Rochester Code, and the law so often vigorously defended by Professor Britton, who "accepted Tissa rather than Buda for the simple reason that it stands first on the page in Adanson's 'Familles,'" saying, "That is priority, I am sure."

After such clear definition of the principle of priority by Professors Britton, Greene, and Underwood, we are now amazed to see from Professor Britton's pen a convincing argument against the uniform selection of the first species as the type of a complex genus. Where shall we look for that long-promised "uniformity" when, in writing of the principle as logically followed by Professor Underwood and more than once by Professor Greene and by Mr. Thomas Howell, Professor Britton now says, "Inasmuch as a great many genera have at their first publication been made to include more than one species, and in a large number of instances some of these, often the first in position, have been used by subsequent authors as the types of additional genera, this latter-day proposition affects an enormously greater number of cases than those which fall properly under the operation of the rule"?[10] And when, continuing his argument against the necessary acceptance of the first species as the generic type, he says "*it is, therefore, clear that there is nothing logical in the proposed extension of the principle*" [italics ours],[11] does he not directly contradict the conclusions of Professor Greene and Professor Underwood? Furthermore, how are such views reconciled with the fundamental principle of the Rochester Code, and with the former statements of Professor Britton himself, who in 1890 emphatically argued of "priority of place," that "that is priority, I am sure"?

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[8] Pittonia **3**: 128. 1896.

[9] Mem. Torr. Bot. Club **6**: 247. 1899.

[10] Science **13**: 588. 1901.

[11] Science **13**: 588. 1901.

When the Rochester Code and its Madison amendments were put forward we were repeatedly told that their *raison d'être* was to establish our plant-names upon a permament basis. Therefore when the *Check List* was published it was naturally supposed that the names there included were final. At great inconvenience to all branches of American botany we have been forced, consequently, to stumble through a most perplexing tangle of ever-changing "permanent" names. If all this confusion and inconvenience were leading us by the shortest course —or by any course—to stability, no one but the short-sighted would complain. It is true that, in spite of their frequent changes from one policy to another, and notwithstanding the utter abandon with which they trifle with the most important principles, the reformers still claim to be bringing us uniformity. How can this be? Professor Underwood stands firmly for priority of place, claiming that the first species in the genus must be taken as the type. Professor Greene has taken the same ground, though openly arguing against some other principles of the Rochester Code. Now, after agitating for years the principle of strict priority and more than once defining his understanding of the term, Professor Britton has published an argument squarely opposed to the uniform acceptance of the first species of a complex genus as the type. Can it be, then, that with such hopeless diversity of opinion on the part of two leading reformers at the same university, they still have sufficient sense of humor to tell us that they are establishing uniformity? If Professor Underwood, following consistently the spirit and text of the Rochester Code, believes in changing "99 per cent." of names; and Professor Britton, abandoning the fundamental principle for which he has so long argued, changes names on a radically different basis, will they not give us systems of names more and more hopelessly unlike?

Professor Britton declares the position taken by Professor Underwood a "latter-day proposition," thus implying that the question of generic types was not seriously considered at Rochester and at Madison. Yet if the Rochester Code is the result of a "very careful consideration," how can this vital matter have been overlooked? However, the Rochester Code tells us that "priority of publication is to be regarded as the fundamental principle of botanical nomenclature," and Professor Britton has said "it is perfectly clear that as long as we allow ourselves a choice of names *in any way*, so long will authors differ in their acceptance and the settling of this important matter be deferred" [italics ours].[12] From these assertions the only logical conclusion is that doubtful cases are to be referred to the principle of priority. The decision between Buda and Tissa, and the determination of the generic type both "allow . . . . a choice of names," and according to the first principle of the Rochester Code priority alone should settle them. The question of Buda and Tissa is one of decision between two generic names for the same plant; the question of the generic type asks which of two or more plants shall bear a given generic name. When these questions have such fundamental similarity, how can a reformer maintain that priority is to decide in one case and not in the other?

When Professor Britton now maintains that the first species of a complex genus is not necessarily the type, and that in such cases the Rochester code allows us to cling to the traditional genera, he at once places himself on record as likewise opposed to the fourth rule of the Rochester Code. This rule reads:

> IV. HOMONYMS.—The publication of a generic name or a binomial invalidates the use of the same name for any subsequently published genus or species respectively.

Let us look, for example, at the case of Mimosa, a name which Professor Britton and other reformers use in its traditional sense. The Linnæan Mimosa, published in the *Species Plantarum*, contained 39 species, the first on page 516, the last on page 523. Of these species only six are now retained in the genus as finally defined by Bentham in 1875 and now generally accepted. The first species now recognized in the Benthamian genus Mimosa is *M. viva*, no. 11 of the *Species Plantarum*. This species is the last one on page 517, and on that page it is preceded by six species, and on page 516 by four species, all of which are now treated as members of other genera. If Tissa has priority over Buda "for the simple reason that it stands first on the page," then surely by the same logic *Mimosa bigemina* and the other five species on page 517 have priority over *M. viva*. And still more clearly *M. viva* is preceded by *M. Lebbeck* (now treated as an Albizzia) and the other species on page 516. Mimosa was published on this page (516) of the *Species Plantarum* as the name of a genus; then *M. Lebbeck*, *M. Inga*, *M. fagifolia*, and *M. nodosa* were published, not only with citations of their previous places of publication, but with brief diagnoses as well. Consequently the publication of the generic name Mimosa and the first of the species, *M. Lebbeck*, satisfies the Rochester requirement for the publication of a genus (see above). Furthermore, the species was treated as a Mimosa subsequent to its original publication in 1753, and it was first removed from the genus by Willdenow in 1806. Therefore, when the name Mimosa in the Benthamian sense is applied by Professor Britton to *M. viva* (and its congeners) while on a preceding page the same generic name had been applied to *M. Lebbeck*, a plant of different generic affinity, he uses a name which is a homonym.

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[12] Jour. Bot. **28**: 372. 1890.

Two fundamental principles of the Rochester Code are thus deserted by the chairman of the Rochester committee on nomenclature, while strongly defended by only one of the original members. And now from Nebraska, which has not long been notable as the seat of ultra-conservatism, comes the announcement, in regard to the recent work of the only consistent member of the original committee, that "it shakes one's faith in the immutability of things to find old friends under unfamiliar names."[13]

The reformers wedded themselves to the principle of strict priority. At the start they ignored the reasoning of those who foresaw where it would lead them. They rushed headlong and short-sighted into the scramble for hidden and obscure names. For a short time they worked harmoniously. Then came misunderstanding and lack of unity. One member of the nomenclature committee disclaims "that there is any obligation to elevate varietal names to specific rank when the [aggregate] varieties themselves are thus promoted."[14] In so doing he opposes the rule of the *Check List* committee which says "that the original name is to be maintained whether published as species, subspecies, or variety." Another member stands for absolute priority and takes a course in which Professor Britton finds "nothing logical." The chairman of the committee now proclaims that priority of place (precedence) is not necessarily final. In so doing he opposes not only the first, but the fourth of the Rochester principles. To every logical and fair-minded scientist who will take the trouble to consider the question calmly and judicially, this woeful diversity in the practices of the committee must be apparent. No one can say today where individual members of the *Check List* committee will stand tomorrow. They have forgotten or ignored the fact that the Rochester Code was to give us permanent names. They have made of it a "personal preference hit-or-miss system." In the words of one of their number, they are "openly at war with their own rules." Is this uniformity? Is this "the day of law"? Is this the high road to a stable nomenclature?

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[13] Science **13**: 833. 1901.

[14] GREENE, E. L., Pittonia **4**: 253. 1901.

Do we sincerely want uniformity, or do we prefer the tangled results of individual interpretation? If the former ideal still appeals to us, why not abandon this restless pursuit of the will-o'-the-wisp? Why not honestly test the combined Berlin rule for genera and Kew rule for species? None of their opponents have given them a fair trial. Until they do can they really judge of their merits?—M. L. FERNALD, *Gray Herbarium, June, 1901.*

FLOWER VISITS OF OLIGOTROPIC BEES. III.

AMONG the oligotropic bees mentioned in BOTANICAL GAZETTE **28**: 36, 215, and **30**: 130, should be included: *Andrena krigiana*, which collects its pollen from *Krigia amplexicaulis; Entechnia taurea*, which is an oligotropic visitor of *Ipomoea pandurata:* and *Anthedon compta*, which gets its pollen exclusively from *Oenothera biennis.*

Species of Melissodes, which usually collect the fine pollen of Compositae, have their scopae dense and quite closely plumose. On the other hand, Emphor, Xenoglossa and Entechnia, which collect the large pollen grains of *Hibiscus lasiocarpus*, *Cucurbita pepo*, and *Ipomoea pandurata*, have their scopae quite loose and thinly plumose. The close relationship of Anthedon to Melissodes, and the fact that the male has quite plumose hairs on his hind tibiae, show that the scopae of the female have recently lost the barbs and have come to be composed of simple bristles. I have wondered why this was so, and have expected to find some peculiarity in the pollen which the bee collects. Now in *Oenothera biennis* the pollen grains are large, trilobed, and connected by cobwebby threads. This condition of the pollen makes the barbs unnecessary if they would not greatly interfere with the collection of this kind of pollen.

Andrena nasonii, mentioned in the first list, is not oligotropic.

In the *Fertilization of Flowers*, p. 570, in discussing the effect of conspicuousness of flowers in inducing insect visits, Müller says:

"The most important deduction to be drawn from them is, that in general anthophilous insects are not limited by hereditary instinct to certain flowers, but that they wander about getting their food on whatever flowers they find it. For if each insect had its own species of flower, as most caterpillars have their own particular food plant, the abundance of insect visits to the plant would not depend at all upon its conspicuousness." Then, after mentioning the case of *Andrena florea* and *Bryonia dioica*, etc., he says: "But these insects do not form 1 per cent. of all the species that I have observed, and even of these cases the restriction is only complete in two."

In my neighborhood, excluding the inquilines, which do not make nests, 30 per cent. of the bees are oligotropic.— CHARLES ROBERTSON, *Carlinville, Ill.*

CURRENT LITERATURE.

BOOK REVIEWS.

Latex and mucilage.

To THE already extensive literature of the laticiferous tissues, Molisch contributes an important addition,[1] differing from its predecessors in giving chief attention to the constitution, both organic and chemical, of the latex itself. In his investigations he used living material and fresh latex, as well as that which had been fixed and stained. Molisch has confirmed and extended the earlier observations of Treub, Johow, and Schmidt on the existence of a plasmic membrane and nuclei in the latex tubes, for demonstrating which he recommends *Euphorbia splendens* and *Poinsettia pucherrima*. He finds the membrane lining the latex vessel and constituting an inner living tube within which the latex is formed like the cell sap. Special examination of the nuclei shows that some nuclei are very different from those of ordinary plant cells, having characters not before known in nuclei of any plant or animal. Molisch calls them *Blasenkerne.* The granular nucleus seems to lie centrally or excentrically in a relatively large globular vacuole, but really the vacuole is in the nucleus, the nuclear sap filling the space between the nuclear material and the membrane. Nuclei of somewhat irregular form are also present. Various phenomena lead to the conclusion that the nuclear membrane is an independent, clearly differentiated organ.

Besides the nuclei there are imbedded in the plasma leucoplasts of different kinds. Some form the elongated starch grains; others ("proteinoplasts") produce proteid granules, a phenomenon which has recently been observed also by Heinricher in Lathraea. Crystals of proteids or proteid-like substances are also produced, not anywhere in the contents of the latex tubes, but by the agency of special plastids or of vacuoles. Molisch also finds elaioplasts and vacuoles responsible for the formation of oil drops.

Into the details of the chemistry of the latex we cannot follow the author. The latex he finds usually acid, rarely neutral, and never alkaline; calcium salts and chlorids are variable in amount; magnesium compounds are abundant and sometimes accumulate in extraordinary quantity; proteids and carbohydrates are so abundant that one must look upon the latex tubes as special reservoirs of these foods.

As the latex is an emulsion, the fine division and consequently great surface of its constituents probably facilitates the absorption of gases and metabolism generally, to an extent hitherto unnoticed. On the rôle of the latex the author promises further publication.

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[1] MOLISCH, HANS: Studien über den Milchsaft und Schleimsaft der Pflanzen. 8vo, pp. viii + 111, *figs. 33.* Jena: Gustav Fischer. 1901. *M* 4.

Because the mucilage tubes of the Liliaceae, Amaryllidaceae, and Commelynaceae are analogous to the latex tubes, Molisch has investigated them. He finds extraordinary nuclei in some of them — filaments 1500µ long by 0.1–0.3µ in diameter; also proteid crystalloids, starch, glucose, and tannins, as in latex tubes, besides a new body, luteofilin, which occurs as sphere crystals in the mucilage of many monocots.—C. R. B.

A manual of bacteriology.

IN 1897, Frederick D. Chester published in the *Annual Report* of the Delaware Agriculture Experiment Station a preliminary arrangement of the species of the genus Bacterium. This work, rearranged and enlarged to include all the groups of bacteria, has now appeared in a valuable *Manual of determinative bacteriology*.[2] While not so voluminous as Migula's great work on systematic bacteriology, this book is by far the most complete classification in English, comprising descriptions of some 780 forms. The system of classification adopted, by means of which related forms may be readily traced out or new species identified, is the same as that first proposed by Migula in Engler and Prantl's *Natürlichen Pflanzenfamilien* (1896), with some minor modifications. In the synopsis of Bacterium and Bacillus, coloration by Gram's method is used as an important differential test. This might be open to criticism, for variation of the Gram staining reaction within a so-called group is well known. It was brought out in a recent study of *B. pyocyaneus* by Roger C. Perkins as follows: "In reactions of the various organisms to Gram's stain, my results did not coincide with those of Jordan and Ruzicka, who note complete decolorization in every case. Of ten varieties studied in this present series, seven decolorized uniformly and regularly when treated by this method, but three retained the color at every trial."[3] On the other hand, Chester has given a subordinate place to formation of gas in the different sugar bouillons, a comparatively constant reaction.

In the section devoted to the terminology of descriptive bacteriology, the author has arranged and illustrated an excellent series of simple terms, capable of expressing definitely in one word the meaning of several sentences of the old style verbose and figurative cultural description. These terms are interesting additions to the bacteriological vocabulary. The criticism of species nomenclature is a point well taken, although no adequate suggestion is made as to how names of forms so closely related as the various kinds of fluorescent bacteria could be made indicative of that fact and yet avoid the trinomial term. What faults may be found in the book, however, are of minor importance in comparison with its value as a reference book, and a supplement to the text-book of every student in a bacteriological laboratory.—MARY HEFFERAN.

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[2] CHESTER, FREDERICK D., A manual of determinative bacteriology. 8vo, pp. vi + 401, *figs. 13*. New York: The Macmillan Co. 1901. $2.60.

[3] Jour. Med. Research 281. 1901.

The flora of Alabama.[4]

DR. CHARLES MOHR has left behind him a most substantial monument. The bulky volume before us contains the botanical records of "forty years of sojourn and wanderings" through the state of Alabama. It may be added that the "wanderings" were by no means aimless, but were those of a keen and tireless observer. Such a mass of observations by a single man is the possession of no other state. It is a pleasure to note that the author was permitted to complete the organization of his notes of a lifetime into permanent and usable form.

The book presents the patient study of a great and interesting area, not by the perfunctory cataloguing of species collected, but by the discussion of the broad biological features which have determined the flora and its distribution. The author evidently fully appreciated the newer aspects of the problems of floras, and has presented to us, in terms of Merriam's life zones and Warming's plant associations, the general ecologic and floristic features of Alabama.

The general discussion occupies 137 pages, and is full of material for the student of phytogeography. After some preliminary historical material, in which the work of such pioneers as Bartram, Buckley, Gates, Peters, Beaumont, and Nevius, are fully noted, the general physiographic features of the state are presented under topography and geology, river systems, and climate. Then follows an account of the general principles of plant distribution, the significance of life zones and of plant associations and formations being explained. These principles are then applied to the flora of Alabama, which is presented in its general character and distribution.

The ecologic relations are considered under the following titles: forest flora, open land or campestrian flora, water and swamp flora, organotopic flora (epiphytic, saprophytic, parasitic, and insectivorous plants), and introduced plants and their influence upon native plant associations. The distribution falls naturally under the two general heads of the Carolinian and Louisianian areas; the former including the mountain region, the table-lands of the Warrior and Coosa basins, the region of the Tennessee river valley, and the region of the lower hill country; the latter including the region of the central pine belt, the central prairie region, and the maritime pine region.

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[4] MOHR, CHARLES: Plant life of Alabama. An account of the distribution, modes of association, and adaptations of the flora of Alabama, together with a systematic catalogue of the plants growing in the state. Contrib. U. S. Nat. Herb. **6**: 1–921. *pls. 1–13*. 31 Jy. 1901.

The systematic catalogue occupies 682 pages, and is a model of painstaking care in the way of bibliography, synonymy, and range. The thallophytes number 1722, and notably full is the list of fungi by F. S. Earle, and the list of lichens. The bryophytes number 166, the pteridophytes 109, the gymnosperms 13, the monocotyledons 681, and the dicotyledons 1782. The total enumeration of species and varieties is 4473. About ten new species are described, but very many described elsewhere are founded on Dr. Mohr's material. The three endemic species are *Trichomanes Petersii*, *Croton Alabamensis*, and *Neviusia Alabamensis*. The sequence is that of Engler and Prantl, and the nomenclature is that of the Rochester code.

It is a matter of great regret that the author was not spared long enough to receive the congratulations of his associates upon the appearance of his monumental work.—J. M. C.

Methods in plant histology.[5]

AS STATED in the preface, this work has grown out of a course in histological technique given by the author to his classes in the University of Chicago and to its non-resident students taking work in this subject through the Extension Division. A series of articles on the same subject published by the author in the *Journal of Applied Microscopy* forms the basis of the present volume.

The first part of the book, about one-third, is devoted to the discussion of apparatus, reagents, and most of the important methods of killing and fixing, staining, sectioning, and mounting plant tissues and the lower forms of plant life. The chapter on apparatus is short, and much could be introduced that would enable the student who has not a complete laboratory equipment before him to save time and material and also produce more perfect results. The chapter on reagents seems unnecessary, as most of the matter is repeated elsewhere in the book. The description of the paraffin method is most complete and very carefully prepared, while the treatment of the celloidin method is hardly adequate, and does not give the more recent improvements that contribute so much to the successful use of this method in plant histology. The treatment of the methods of killing, fixing, and staining is admirable.

Part II is devoted to the study of types of the various groups of plants systematically arranged and illustrated by specimens easily collected by any one familiar with the main divisions of the plant kingdom. The directions for the treatment of the material used in these studies are excellent, and the specimens judiciously selected. The treatment of the spermatophytes is the most comprehensive in the selection of material and in its preparation. The author, by his careful discussion of the various methods in the preparation of material emphasizes what is too often neglected in general histological studies, particularly of the lower forms, the careful preparation of material for examination. Much of the histological work with classes is misleading and useless because the teacher fails to appreciate this point. The student who learns to make a proper use of the best methods early in his course will be well repaid when at a later period he begins more critical studies. A convenient list of formulae for reagents is placed at the end of the volume.

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[5] CHAMBERLAIN, CHARLES J.: Methods in plant histology. 8vo. pp. vi+159. *figs. 74.* Chicago: The University of Chicago Press. 1901. $1.50.

The technique of the book is good, and the illustrations well selected, a few of them being photomicrographs of excellent preparations. The work is a most acceptable contribution to the growing list of laboratory manuals.—M. B. THOMAS.

MINOR NOTICES.

JAMES R. GOW[6] has published a preliminary list of the flowering plants of Adair county, Iowa.

WILDEMAN and DURAND[7] have issued a further publication on the Congo flora. It consists of the first fascicle of an enumeration of plants collected by Alfred Dewèvre in 1895–6 in the state of Congo, and contains from Ranunculaceae through Leguminosae, with descriptions of new species. A notice of the previous series may be found in BOT. GAZ. **31**:70. 1901.—J. M. C.

T. HEDLUND[8] has published a monograph of the genus Sorbus, which further rehabilitates a Linnean genus long included in Pirus. The author recognizes 58 species, and discusses them in great detail, with the help of text illustrations of venation, pollen grains, etc. He also includes subspecies and hybrids. Some ten or twelve North American species are involved.—J. M. C.

THE FIRST part of the second volume of Wiesner's *Rohstoffe des Pflanzenreiches* has just been issued.[9] It contains part of the seventeenth section on *woods*, newly elaborated by Dr. Karl Wilhelm with the assistance of Dr. S. Zeisel, who contributes the chapter on the chemistry of wood. The structure of woods and their physical and chemical qualities are described in 51 pp., followed by a synopsis (90 pp.) of the more important plants whose wood is used in the arts. A seventh chapter (incomplete) is to describe the microscopic characters of the most widely used woods.—C. R. B.

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[6] Proc. Iowa Acad. Sci. **8**: 1–8. 1901.

[7] Annales du Musée du Congo. Botanique. III. Reliquiae Dewevreanæ. Fasc. 1. Bruxelles, May, 1901.

[8] Monographie der Gattung Sorbus. Kongl. Svenska Vetensk.-Acad. Handl. **35**: 1–147. 1901.

[9] WEISNER, JULIUS: Die Rohstoffe des Pflanzenreiches. Versuch einer technischen Rohstofflehre des Pflanzenreiches. Second ed. Lieferung 6. 8vo. pp. 1–160. Leipzig: Wilhelm Engelmann, 1901. *M*5.

The last issue of the *Minnesota Botanical Studies* (**2**:537–655. 1901) contains the following papers: E. M. Freeman, "A preliminary list of Minnesota Uredineae," a little over 100 species being included; DeAlton Saunders, "A new species of Alaria," from the Californian coast; F. K. Butten, "A preliminary list of Minnesota Xylariaceae," including 19 species; W. A. Wheeler, "A contribution to the knowledge of the flora of the Red river valley in Minnesota," 325 species being listed, with eight excellent heliotype plates of plant formations; H. B. Humphrey, "Observations on *Gigartina exasperata* Harv.," a histological study, with one heliotype plate; W. G. Fanning, "Observations on the algae of the St. Paul city water;" W. A. Wheeler, "Notes on some plants of Isle Royale;" D. Lange, "Revegetation of Trestle island;" J. C. Arthur and E. W. D. Holway, "Violet rusts of North America," with one plate; H. L. Lyon, "Observations on the embryogeny of Nelumbo" with three plates, reviewed in the Botanical Gazette for October.—J. M. C.

That fires are not always so detrimental as they seem is disclosed by a reading of the second edition of the phytogeography of Nebraska.[10] The first edition has been reviewed in this journal,[11] and a statement as to the new material is all that is needed here. A comparison of the two editions shows that the entire book has been essentially revised and brought up to date, although the table of contents reads much the same in the two editions. Among the more important additions are a full discussion of methods for the determination of the frequence and abundance of species, a brief treatment of the primitive flora of the great plains, and the treatment of floral and vegetation elements and of accessory biological characters. Throughout the detailed chapters on the formations, much new material, the result of three years' further labor, is added. In the review of the first edition, the importance of this contribution to ecological workers was stated. Now that the book has been in actual use for four years, it is possible to speak yet more highly of its value. It is not too much to say that it is the most important and valuable work that has yet appeared in the field of American phytogeography.—H. C. Cowles.

NOTES FOR STUDENTS

S. Yamanouchi[12] has described and figured bodies in the dividing pollen mother cell of *Lilium longiflorum*, which stain deeply, are centers of radiation, and come to occupy a position at the poles of the nuclear spindle. He regards them as undoubtedly centrosomes.—J. M. C.

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[10] Pound, Roscoe, and Clements, Frederic E.—The phytogeography of Nebraska. I. General Survey. 8vo. pp. 442, with four maps. Lincoln, Nebraska: The University Publishing Co. 1900. Second edition.

[11] Bot. Gaz. **25**:370. 1898.

[12] Einige Beobachtungen über die Centrosomen in den Pollenmutterzellen von *Lilium longifolium*. Beihefte Bot. Centralbl. **10**:310–303. *pl. 1.* 1901.

MISS MARIA DAWSON reports the results of three years' experimentation to determine the economic importance of nitragin, the commercial culture of the nodule organisms of Leguminosae. Her conclusion is "that for peas grown upon ordinary garden soil, peat, clay, or loam inoculation with nitragin is useless and superfluous, whilst upon gravelly soils a small increase in crop results from its use."[13]—C R. B.

ELIZABETH DALE[14] has studied the aerial tubers which are often very prominent in species of Dioscorea, notably *D. sativa*, in which they are said to become six or more inches in diameter. A study of their origin seems to indicate that they are stem structures, with conspicuous powers of propagation. In fact, the author ventures the statement that "the abundant formation of auxiliary tubers in many species of Dioscorea seems as if it were connected with the fact that these plants do not appear to form seed readily."—J. M. C.

DUSÉN has studied the byrological collections of the Swedish polar expedition under Dr. A. G. Nathorst in 1899. The localities visited on east Greenland extend from Pendulum island (74° 40′ N.) to Cape Stewart (70° 30′ N.), about 150 miles north and south of Cape Parry. The island of Jan Mayen was also visited. In this work he has had the assistance of Dr. H. W. Arnell on Bryum and Plagiobryum, and of Herr C. Jensen on Dicranum and Sphagnum. *Bryum subnitidulum*, *B. Dusenii*, *B. minus*, *B. Groenlandicum* and *B. Jan Mayense* are described by Arnell as new species, and the sporophyte of *B. obtusifolium* is fully described for the first time.[15]—C. R. B.

IT WAS OBSERVED by Sachs that when orthotropous roots, not too young, are inverted, they do not return to the vertical but become plagiotropous. Němec finds a satisfactory explanation[16] of this in the alteration of the receptive apparatus described in his previous paper,[17] thus confirming his views as to the nature of the perceptivity of typical roots, as well as Noll's idea, arrived at from theoretical considerations, that alterations in the response to directive stimuli have their source in an alteration of the receptive structure. He has observed, coincident with this induced plagiotropism, a change in the topographic relations of the quality of the sensitive plasmic layer. The difference between the original and the newly assumed structure is just the difference between that found in orthotropous roots and normally plagiotropous ones.—C. R. B.

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[13] Annals of Botany **15**: 511–519. 1901.

[14] On the origin, development, and morphological nature of the aerial tubers in *Dioscorea sativa*. Ann. of Bot. **15**: 491–501. *pl. 26*. 1901.

[15] Bihang till Svenska Vet. Akad. Handl. **27**: 1–71. *pls. 4*. 1901.

[16] Berichte deutsch. bot. Gesells. **19**: 310–313. 1901.

[17] Jahrb. f. wiss. Bot. **36**: 80. 1901. See also BOT. GAZ. **32**: 145. 1901.

A SHORT TIME since reference was made in this journal to the question of nomenclature in phytogeography.[18] It is interesting to read in this connection the translation of Professor Flahault's address at the Paris Congress[19] of 1900. While many may object to the arbitrary usage of the various terms suggested by Flahault, all will agree that the general questions at issue are made clearer, and we shall await the more impatiently the final decision of a competent committee. It seems questionable to the reviewer, however, whether the nomenclature problem can be settled by a committee, or even a convention. An arbitrary set of terms often acts to prevent a real advance of knowledge, if strict adherence is given to them. Already the terms zone, region, and association have rather definite meanings in the minds of active phytogeographers. Even the much vexed word "formation" is being more commonly used in the original and broader sense, as more inclusive than the word "association." Perhaps other terms also will become more definite in a perfectly natural way.—H. C. COWLES.

W. H. LANG in a late paper[20] has given a preliminary account of some experimental work on wild plants of a species of Anthoceros, in which he has demonstrated that by mutilating very young unopened sporophytes and bringing the cut surfaces in contact with soil under certain conditions of moisture, temperature, and light, bud-like outgrowths are produced from the vegetative cells that lie between the sporogenous region and the external layer. The cells in this region are the least specialized of all in the capsule. They become to some degree isolated in position by the decay of the sursounding tissue. The general sequence of the early divisions in the cells giving rise to the so-called prothallial growths are said to be "closely parallel to the early stages of germination of the spores of Anthoceros." His cultures were carried no further than to the production of a "bud-like stage," which produced rhizoids. The result would he more convincing if he had obtained flat prothallia bearing reproductive organs. This is the first discovery of apospory recorded for any liverwort, although found in a number of mosses and ferns.—FLORENCE M. LYON.

THE IMPORTANT WORKS of Stahl and of MacDougal and Lloyd on mycorhiza have been reviewed in this journal.[21] Mention should also be made of the work of Hesselman[22] on the mycorhiza of arctic plants. Boreal forms have been but little studied in this connection, and it might be supposed that the more xerophytic climatic conditions would work against the root fungi. Many plants, however, are found to possess mycorhiza in considerable abundance. Salix, various ericads, Dryas, Diapensia, and other species appeared much like more southern forms. W. Magnus has made an important cytological contribution[23] to the mycorhiza literature. He finds that the endotropic mycorhiza of Neottia is of two types, which differ in position, structure, and function. Four to six layers of cells immediately within the exodermis contain fungal hyphae. In the outer and inner layers of these cells the hyphae are thin-walled, and the fungi are digested by the host plant; ultimately the fungal threads degenerate, forming masses which also contain parts of the cell protoplasm. These masses Magnus regards as excreted products. In contrast to the above the more centrally located hyphae are thick-walled and remain vigorous throughout, not being digested by the host; these hyphae have haustoria and are regarded as parasitic on the orchid. This study thus gives still another view as to the significance of endotropic mycorhiza. Magnus treats in detail the cytology of the hypertrophied host cells, and at the close of the paper gives an excellent bibliography of the mycorhiza literature.— H. C. COWLES.

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[18] BOT. GAZ. **31**: 361. 1900.

[19] Bull. Torr. Bot. Club **28**: 391–409. 1901.

[20] On apospory in *Anthoceros laevis*. Ann. of Bot. **15**: 503–510. *pl. 27*. 1901.

[21] BOT. GAZ. **30**: 68. 1900.

[22] Bihang till K. Svensk. Vet. Akad. Handl. **26**:—. 1900. (See Bot. Centralb. **86**: 239. 1901.)

ITEMS OF TAXONOMIC interest are as follows: E. L. GREENE (Pittonia 4:285–320. 1901) has described 17 new species of Viola, 12 of Cerastium, 5 of Rumex, 8 of Lesquerella, 3 of Draba, and 7 of Lacinaria.—J. K. SMALL (Torreya 1:73–75. 1901.) has discussed Juncoides in the southeastern states, describing a new species; has described (*idem* 97) a new Crataegus from Florida; also (*idem* 107–108) a new Chamaelirium; and (*idem* 67) a new Alleghanian Rudbeckia.—E. P. BICKNELL (*idem* 102–105) has described 2 new eastern species of Lespedeza.—B. D. GILBERT (Fern Bull. 9:53–54. 1901) has described a new Asplenium from Kamchatka.—F. S. EARLE (Muhlenbergia 1:9–17. 1901) has written upon some fungi from Porto Rico, describing 11 new species and 1 new genus (*Cercosporidium*) of the Dematiaceae.—W. N. SUKSDORF (Bot. Monatss. 19:91–93. 1901) has described new species of Sisyrinchium, Potamogeton, Juncus, Deyeuxia, Melica, and Equisetum, from Washington.—THEO. HOLM (Ottawa Nat. 15:110–111. 1901) has described 3 new Canadian species of Gentiana.—WILDEMAN and DURAND (Bull. Herb. Boiss. II. 1:839. 1901) have described a new genus (*Bosqueiopsis*) of Urticaceae from the Congo region.—SCHMIDLE and WELLHEIM (*idem* 1007-1012, *pl. 13*) have described a new genus (*Rhodoplax*) of Pleurococcaceae.—H. MIEHE (Ber. deut. bot. Gesells. 19:434–441. *pl. 21*. 1901) has described a new genus (*Crapulo*) of marine Flagellates.—J. MATSUMURA (Bot. Mag. Tokyo 15:67. 1901) has described a new Formosan genus (*Alniphyllum*) of Styracaceae.—G. LOPRIORE (Malpighia 14:435 and

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[23] Jahrb. für wiss. Bot. 35: 205–272. 1900.

448. 1901) has described two new African genera (*Argyrostachys* and *Sericostachys*) of Amarantaceae.—H. and P. SYDOW (Hedwigia Beibl. **40**: 62–65. 1901) have described a new African genus (*Hapalophragmium*) of Uredineae.—FR. FEDDE (Engl. Bot. Jahrb. **31** : 30–133. 1901) has taken up the Nuttallian genus Mahonia, recognizing 37 species, 7 of which are new.—SCHMIDLE (*idem* **30** : 246, 247, and 253) has described two new African genera (*Myxoderma* and *Chondrogloea*) of Stigonemataceae, and a new African genus (*Chaetonella*) of Cladophoraceae.—J. K. SMALL (Bull. Torr. Bot. Club **28** : 356-361. 1901) has described 8 new shrubs and trees from the southern states, and also a new genus (*Brayodendron*) to include *Diospyros Texana*; and has also (*idem* 451-453) discussed *Dasystoma flava* and some related species, describing two as new.—R. M. HARPER (*idem* 454–484) has described new species of Rhynchospora, Viola, Dicerandra, and Baldwinia, from Georgia.—V. S. WHITE (*idem* 421–444. *pls. 31–40*) has published a revision of the Tylostomaceae of North America, describing 10 new species and including one new genus (*Dictyocephalos*) described by L. M. Underwood.—P. A. RYDBERG (*idem* 499–513), in continuing his studies of the Rocky mountain flora, has published new species of Trifolium, Vicia, Primula, Cuscuta, Monarda, Castilleia, Pentstemon, Sambucus, and of 9 genera in the Compositae.—GEORGE MASSEE (Jour. Linn. Soc. **35**: 90–118, *pls. 4–5*. 1901) has published the second part of his redescriptions of Berkeley's types of fungi, including all the species of Discomycetes and Hysteriaceae of which type specimens exist at present in the Kew herbarium.—J. M. C.

NEWS.

DR. ROLAND THAXTER has been promoted to a professorship of cryptogamic botany at Harvard University.—*Science.*

WE REGRET to announce the death of the young English phycologist William West, who died in India ,from cholera, at the age of twenty-six years.

AN EXCELLENT biographical sketch and portrait of the late Dr. Charles Mohr appear in the September number of *Plant World.* It is written by Professor S. M. Tracy.

DR. A. F. W. SCHIMPER, professor of botany in the University of Basle, and widely known for his monumental *Pflanzengeographie*, died on September 9, in his forty-sixth year.

IN THE OCTOBER number of the *Journal of Applied Microscopy* there is an interesting illustrated account of the botanical laboratory and gardens of the Tokyo Imperial University, by Kiichi Miyake.

A BIOGRAPHICAL SKETCH of Professor T. C. Porter, with an excellent artotype portrait, was published in the July number of the *Bulletin of the Torrey Botanical Club*, having been prepared by Dr. N. L. Britton.

MISS S. M. HALLOWELL, professor of botany at Wellesley College, has been given leave of absence for the year, and the work of the department will be under Miss Clara E. Cummings, assistant professor of botany.—*Science.*

WE HAVE LEARNED that the herbarium of Theodor von Heldreich, professor of botany and director of the Botanic Gardens, Athens, is for sale. It contains approximately 20,000 species, and richly represents the floras of Greece, Asia Minor, and Egypt. It contains also hundreds of types and authentic specimens of new species described by Heldreich in the works of Boissier.

PROFESSOR ALEX. P. ANDERSON, formerly in charge of plant physiology in the University of Minnesota, has been appointed Curator of the herbarium of Columbia University, to fill the position made vacant by the appointment of Dr. Howe to the Garden staff. Professor FRANK S. EARLE, formerly of the Alabama Polytechnic Institute, has been appointed assistant curator in charge of the collection of fungi at the New York Botanical Garden.

AN ACCOUNT of the opening of the new botanical department at Glasgow University appears in the *Annals of Botany* for September last. It was a part of the celebrations on the ninth jubilee of the university, and the opening address was made on June 13, by Sir Joseph Hooker, whose father had been for twenty years the professor of botany at Glasgow. He was followed by Lord Lister and Professor Bayley Balfour in proposing a vote of thanks for the address.

AT THE DENVER meeting of the Botanical Society of America a committee, consisting of Drs. Trelease, Britton, and Robinson, was appointed to investigate and report upon the condition of the National Herbarium. The following resolution was passed: "That it is the present policy of the society to accumulate invested funds until the annual income, interest and dues, is at least $500, and then to use such income yearly, or at greater or less intervals, as circumstances may dictate, for the best advancement of botanical knowledge."

THE SUBJECTS for the Walker prizes in Natural History for the next two years have been announced. For 1902 the botanical subject is "Nuclear fusions in plants," besides a general subject entitled "The reactions of organisms to solutions, considered from the standpoint of the chemical theory of dissociation," which may just as well be competed for by a plant physiologist. For 1903 the subject is "A monograph of any genus or group of thallophytes." For detailed information as to the conditions of competition address Glover M. Allen, Secretary, Boston Society of Natural History, Boston, Mass.

THE EXECUTIVE COMMITTEE of the 11th Congress of Naturalists and Physicians has asked that the following announcement be made: The Congress will convene at St. Petersburg on January 2, 1902, and continue until January 12. General sessions will be held January 2, 8, and 12; and sectional meetings on the other days, botany constituting a distinct section. Those wishing to be present as members should send their names and addresses, with the membership fee (3 roubles), also indicating their section, to the Executive Committee of the Congress, University, St. Petersburg, not later than December 15.

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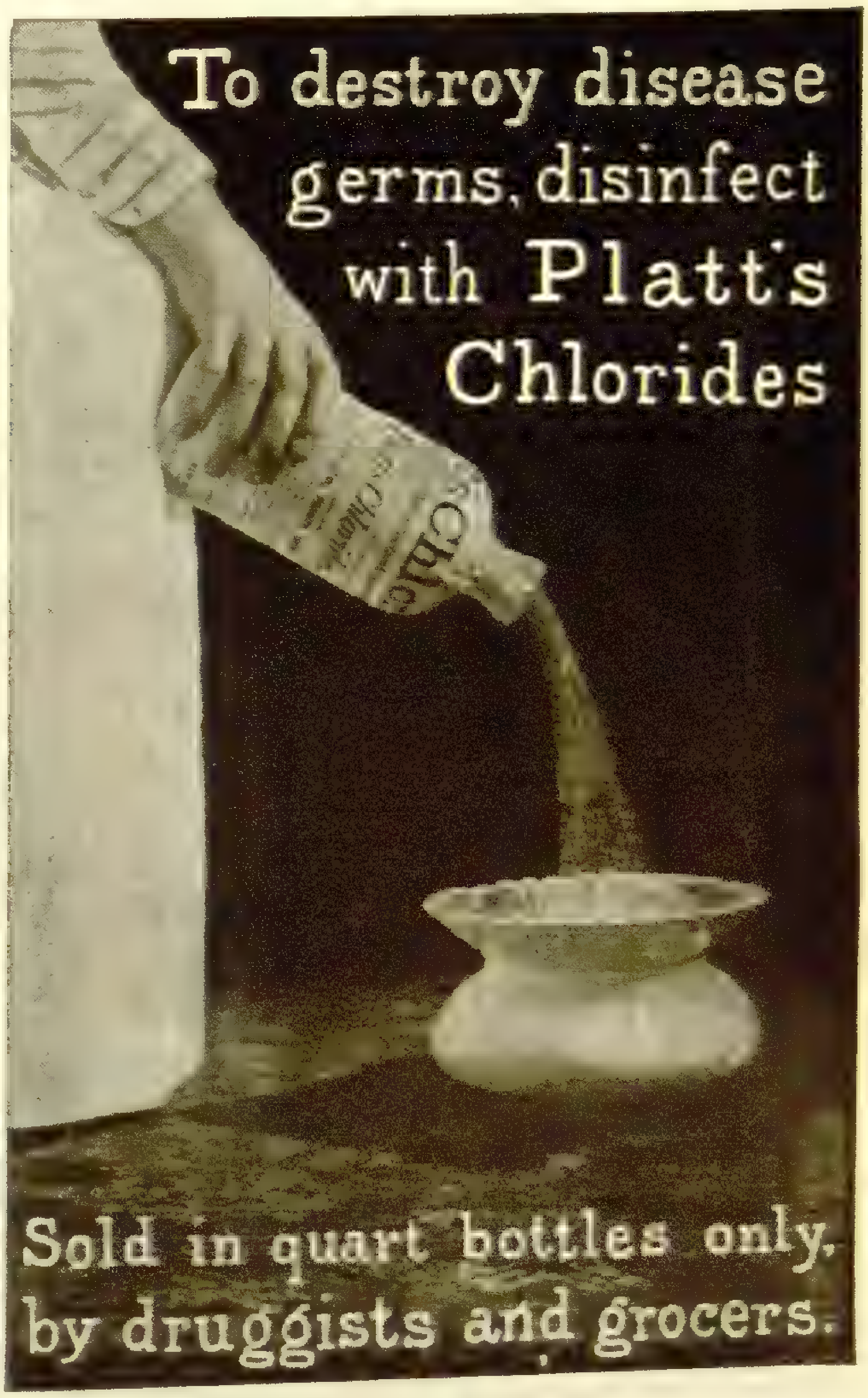
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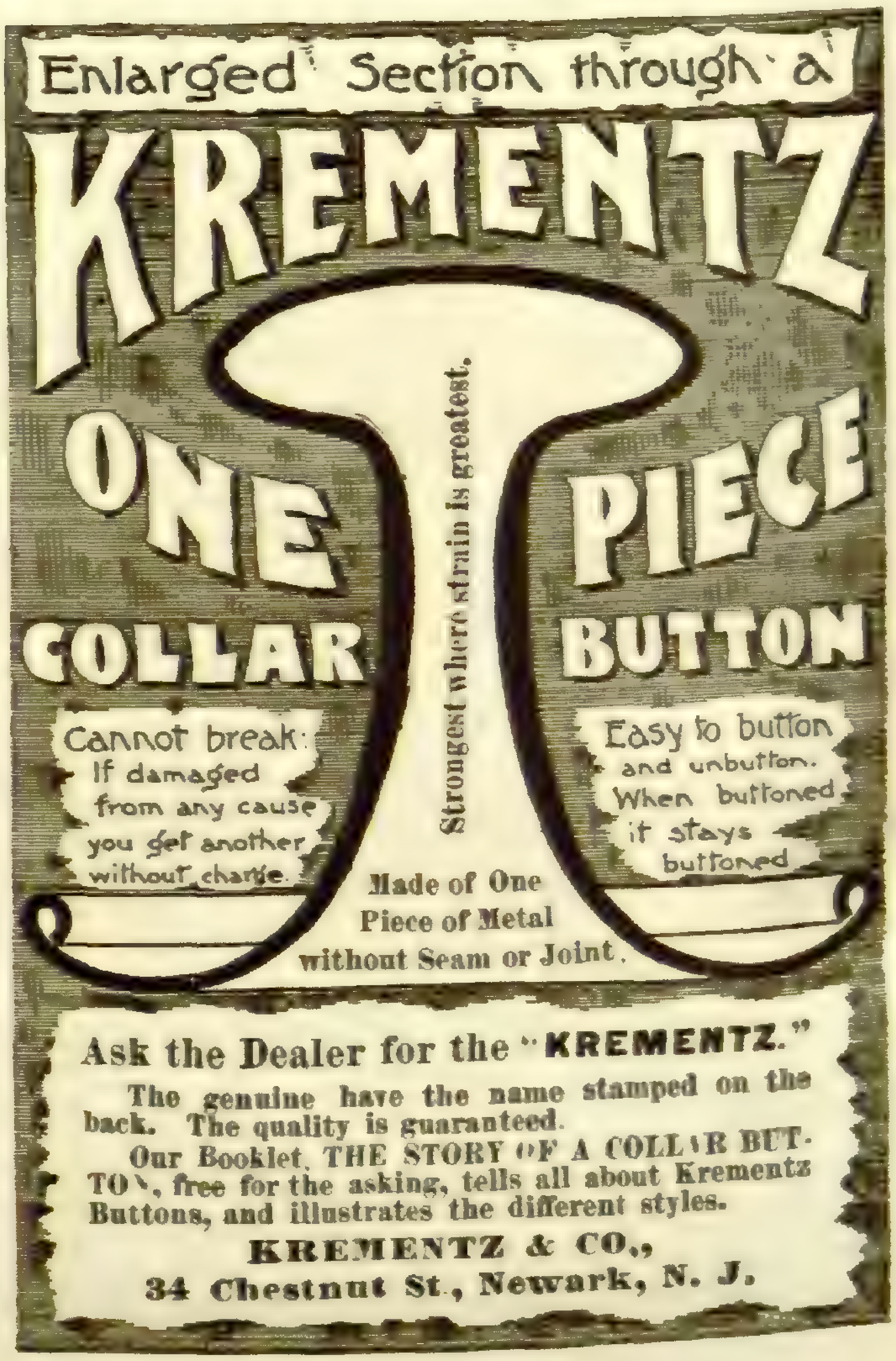
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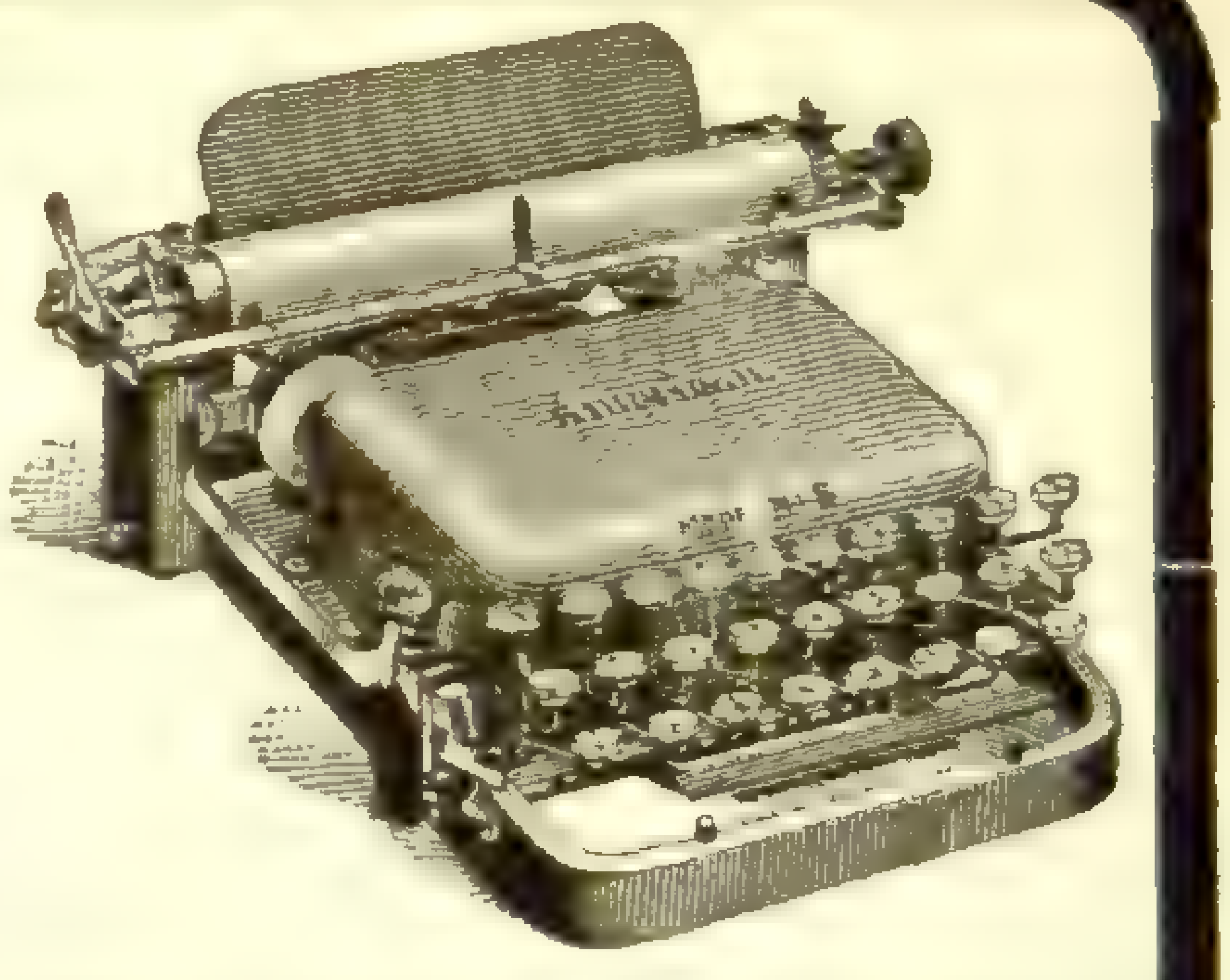

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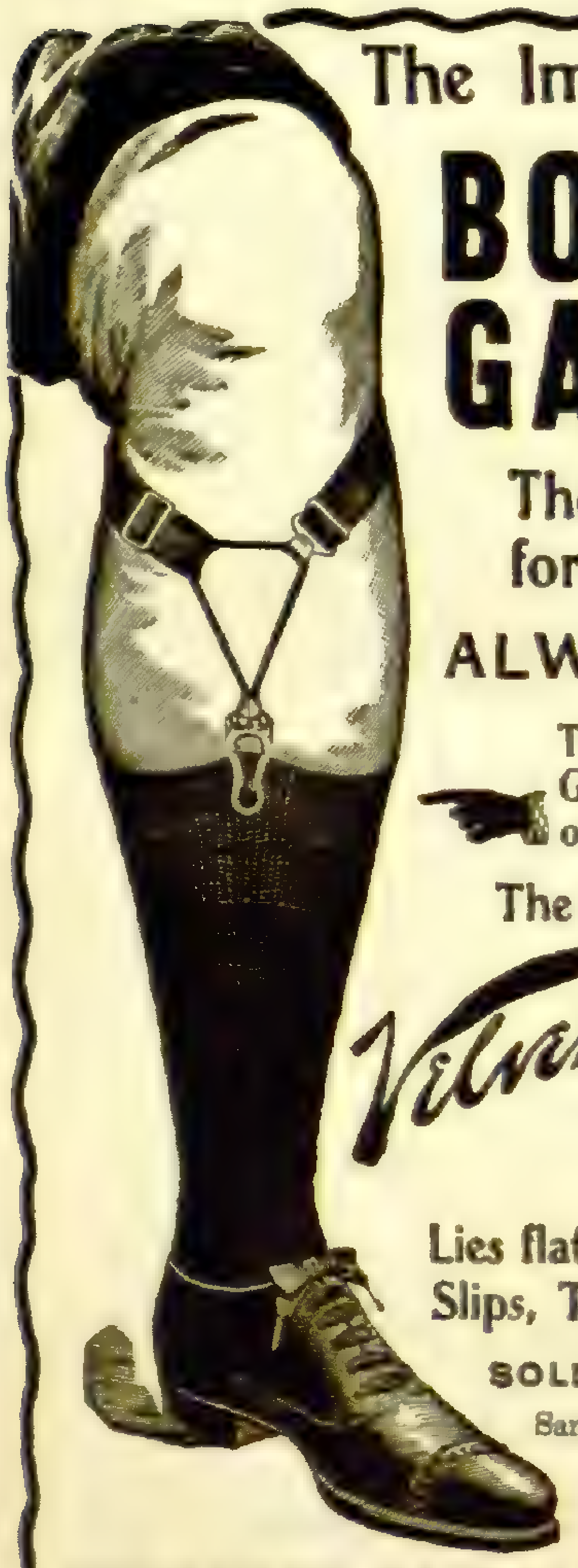

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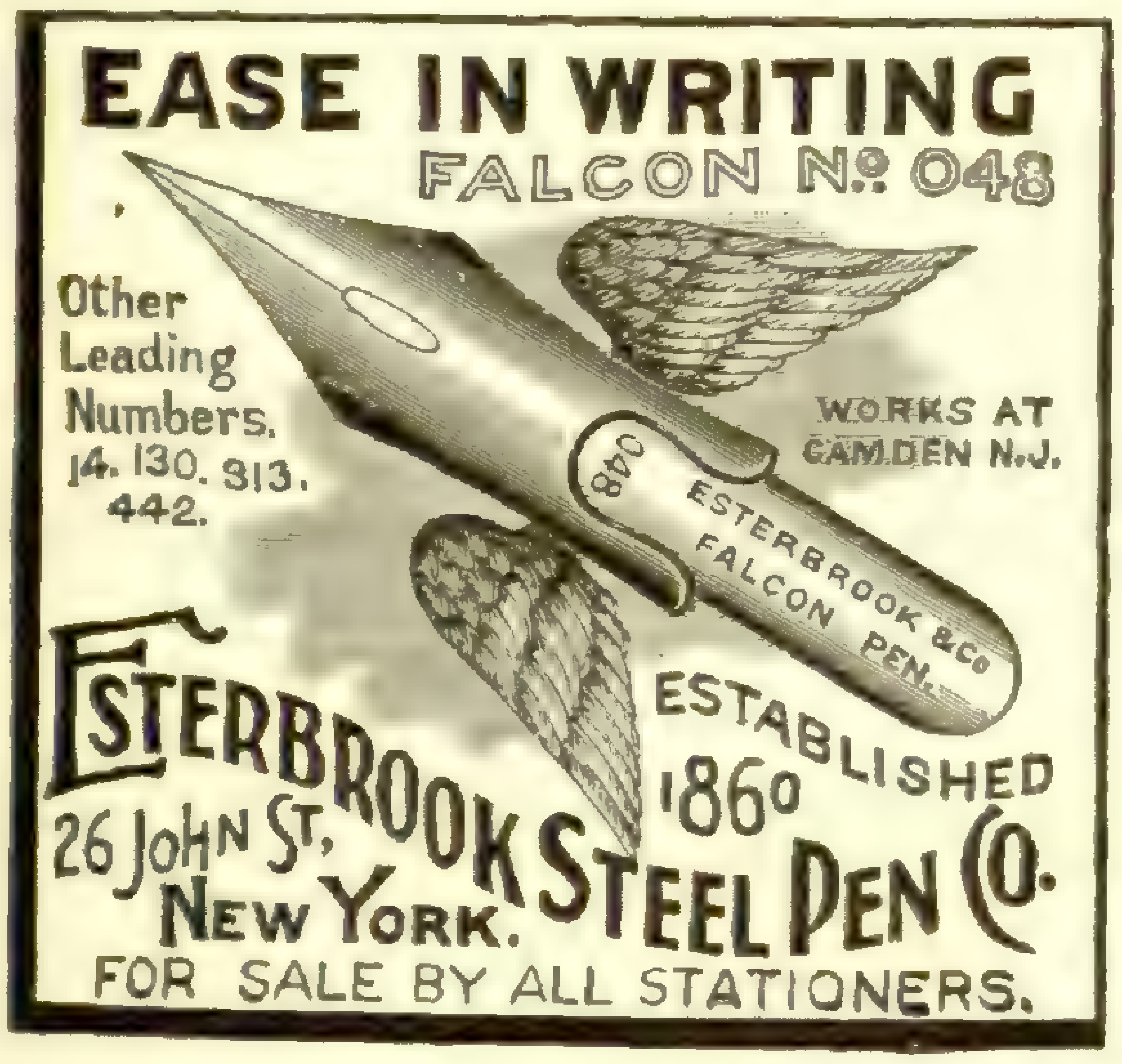
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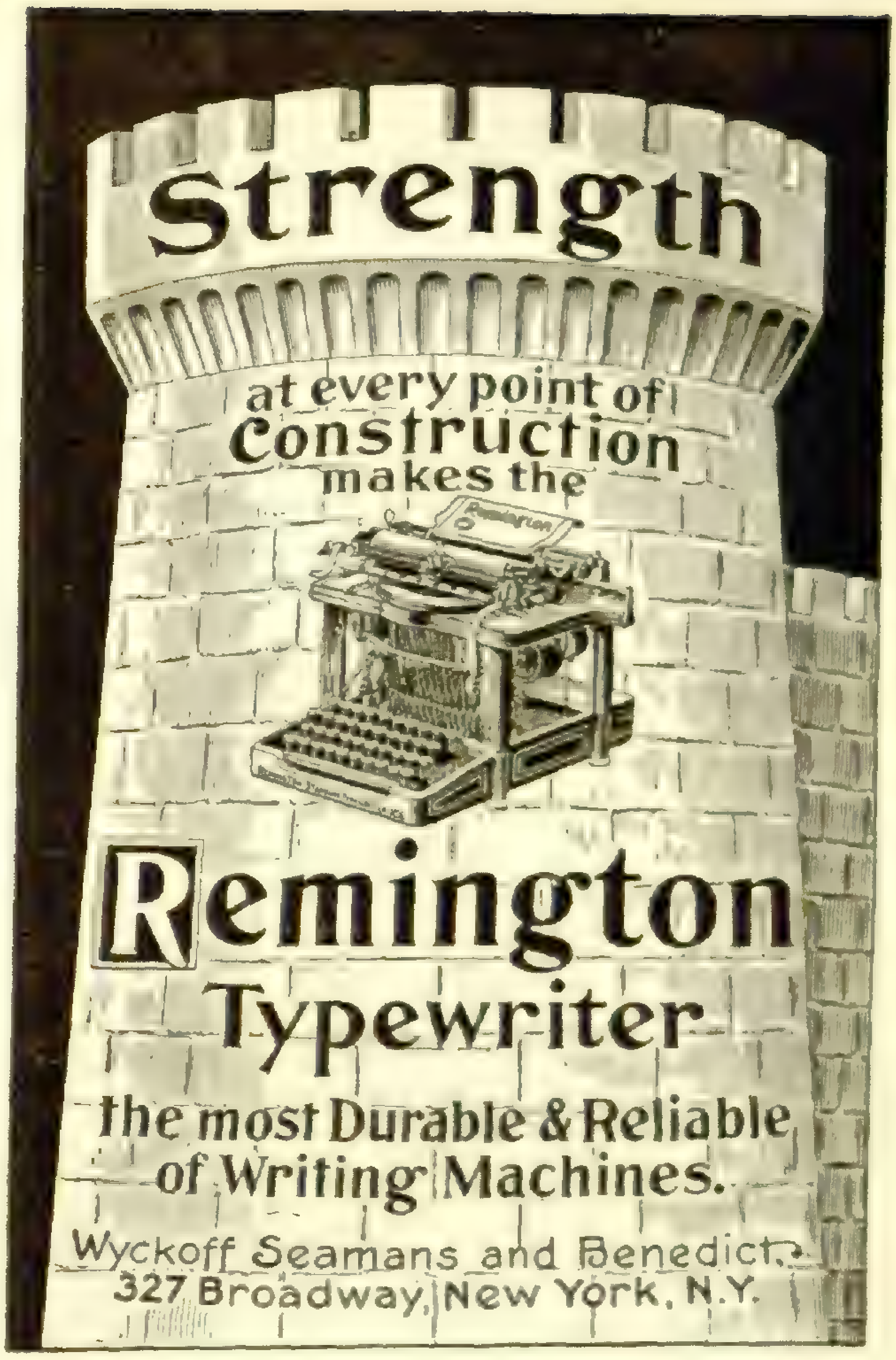
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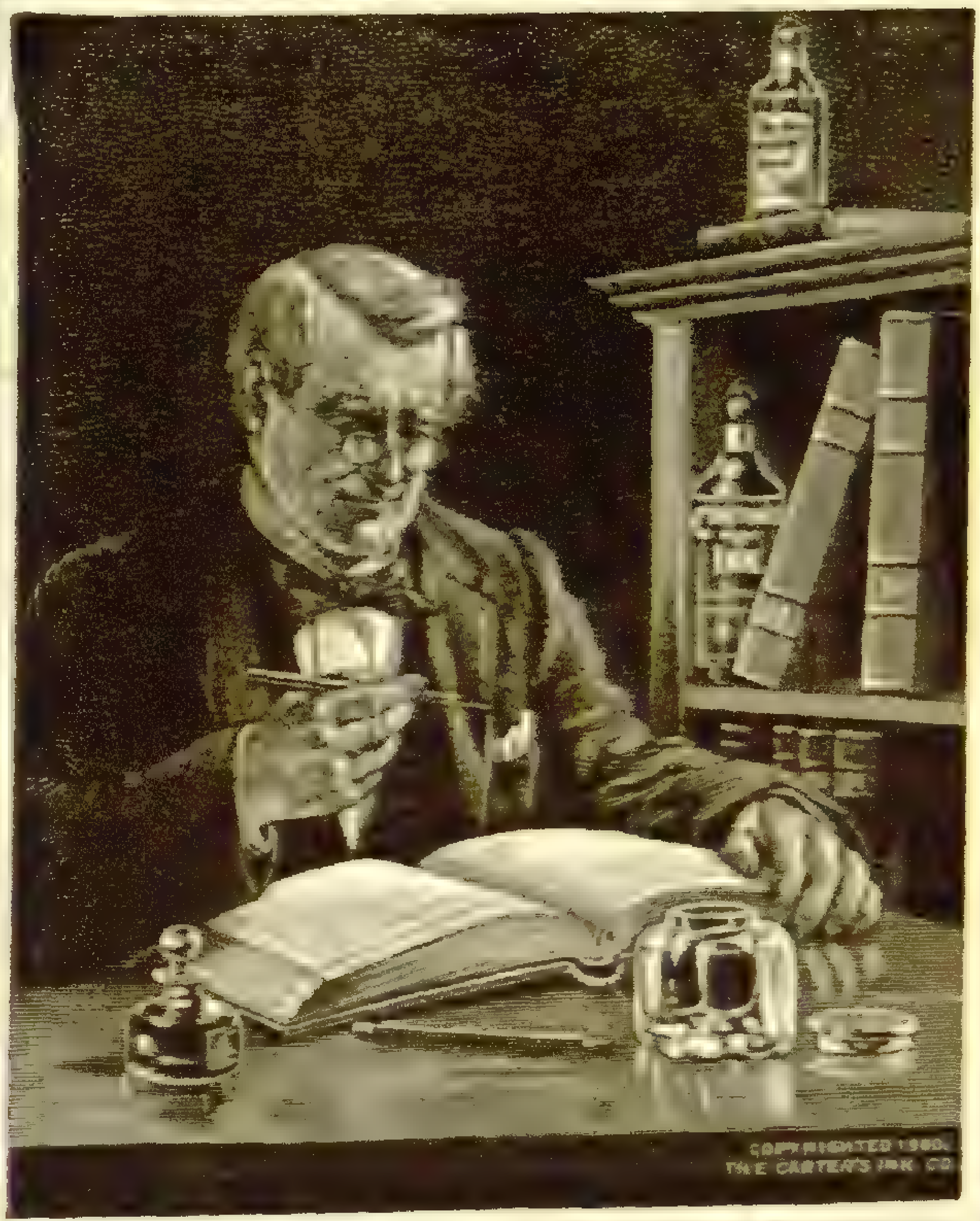
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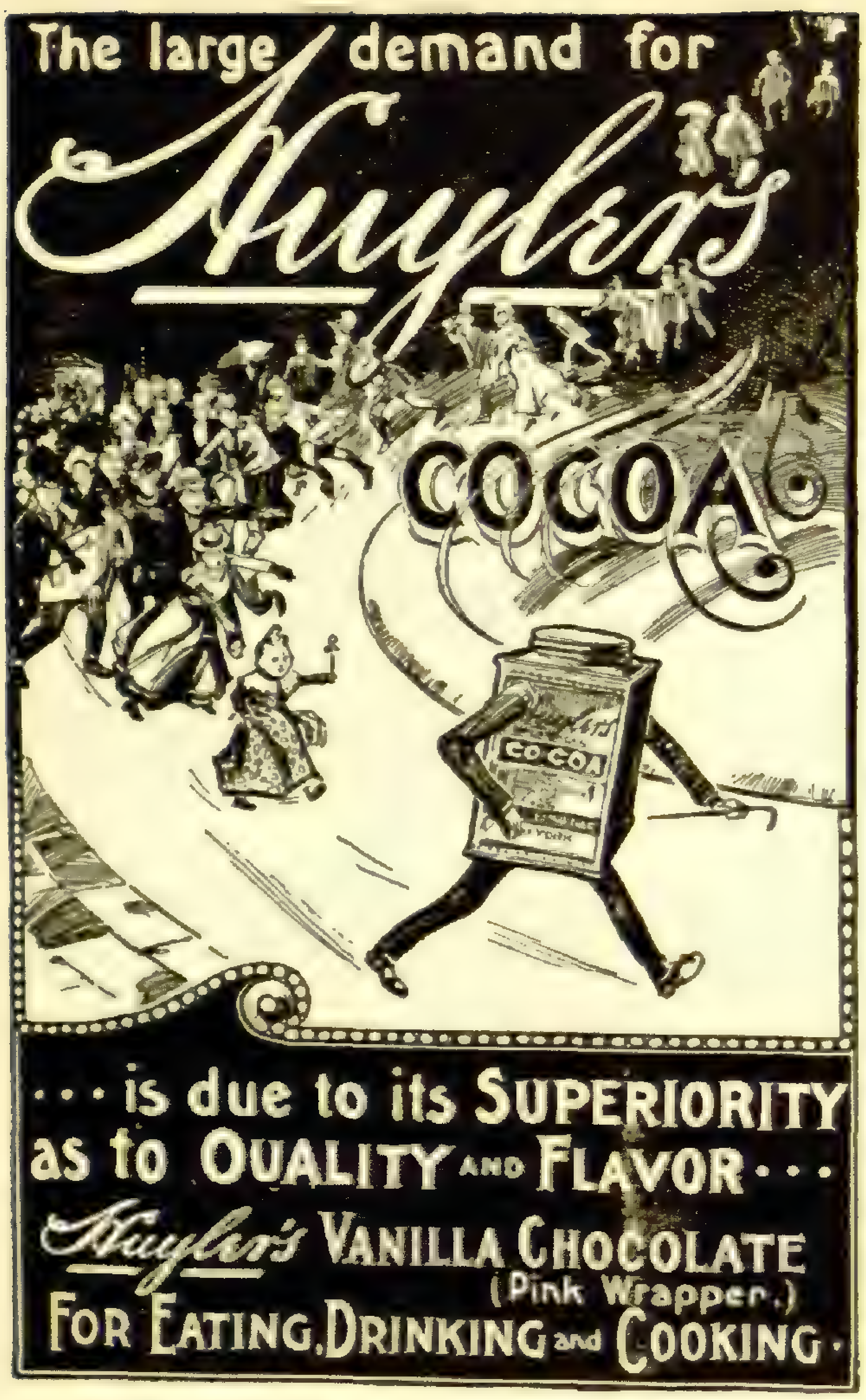

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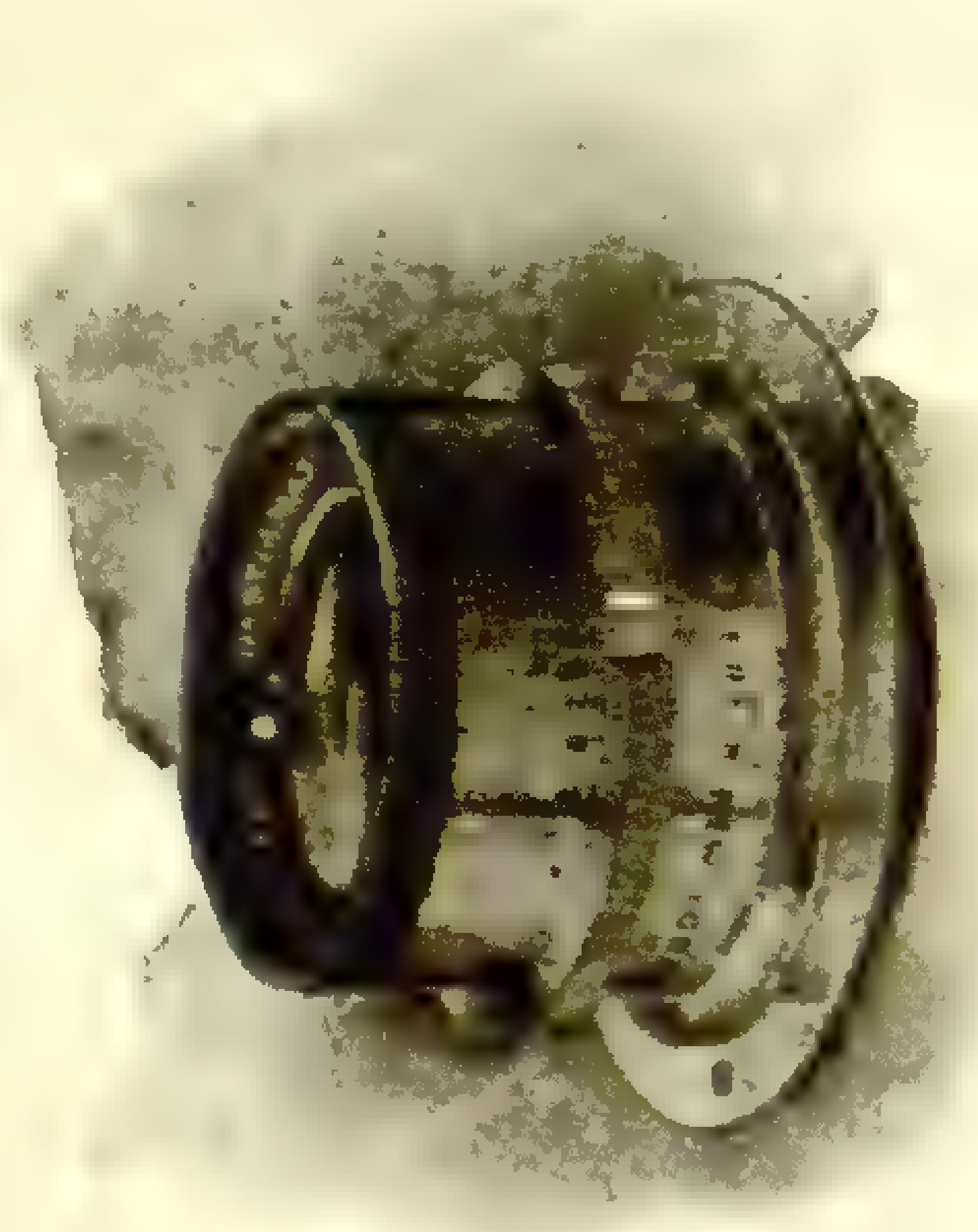

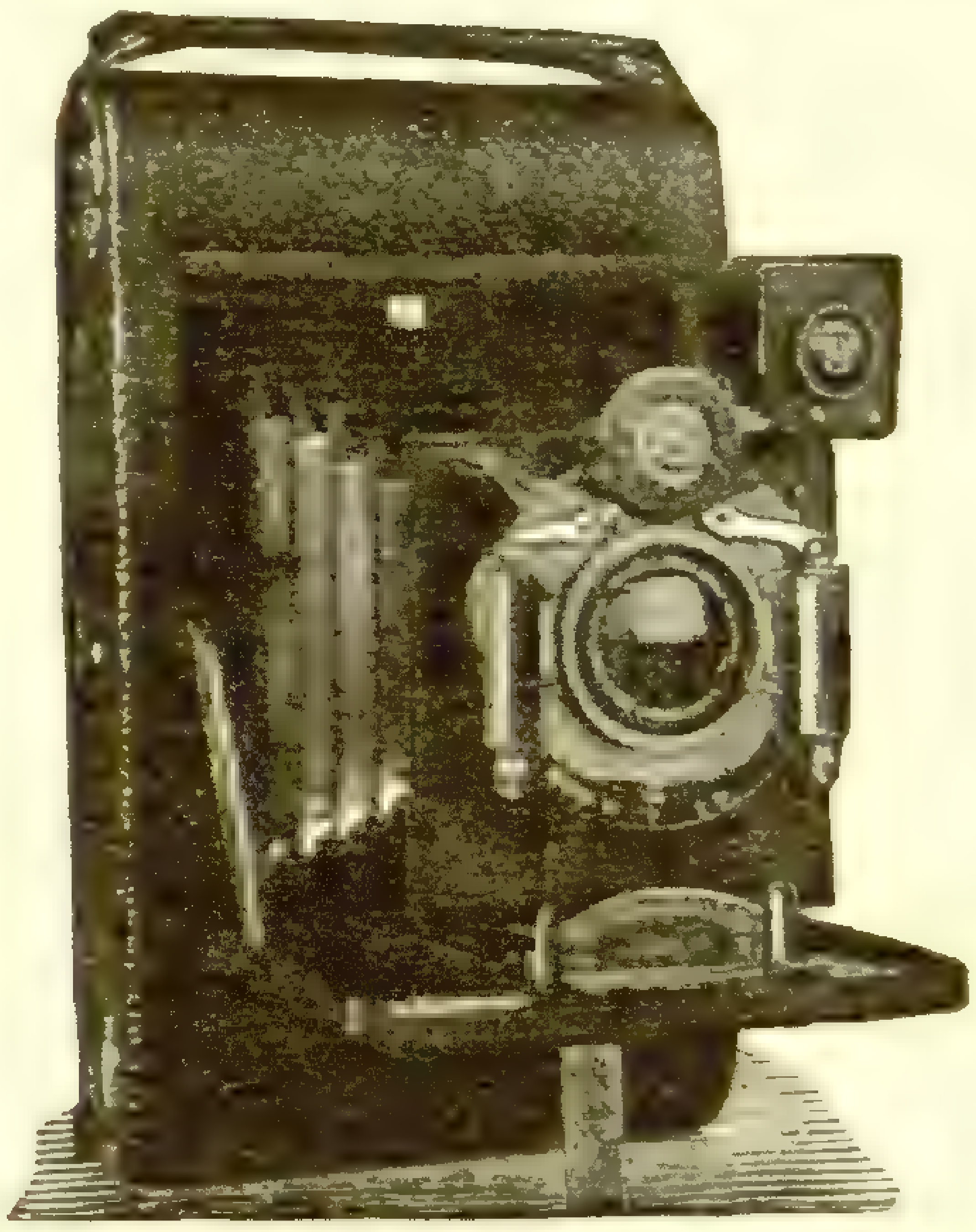

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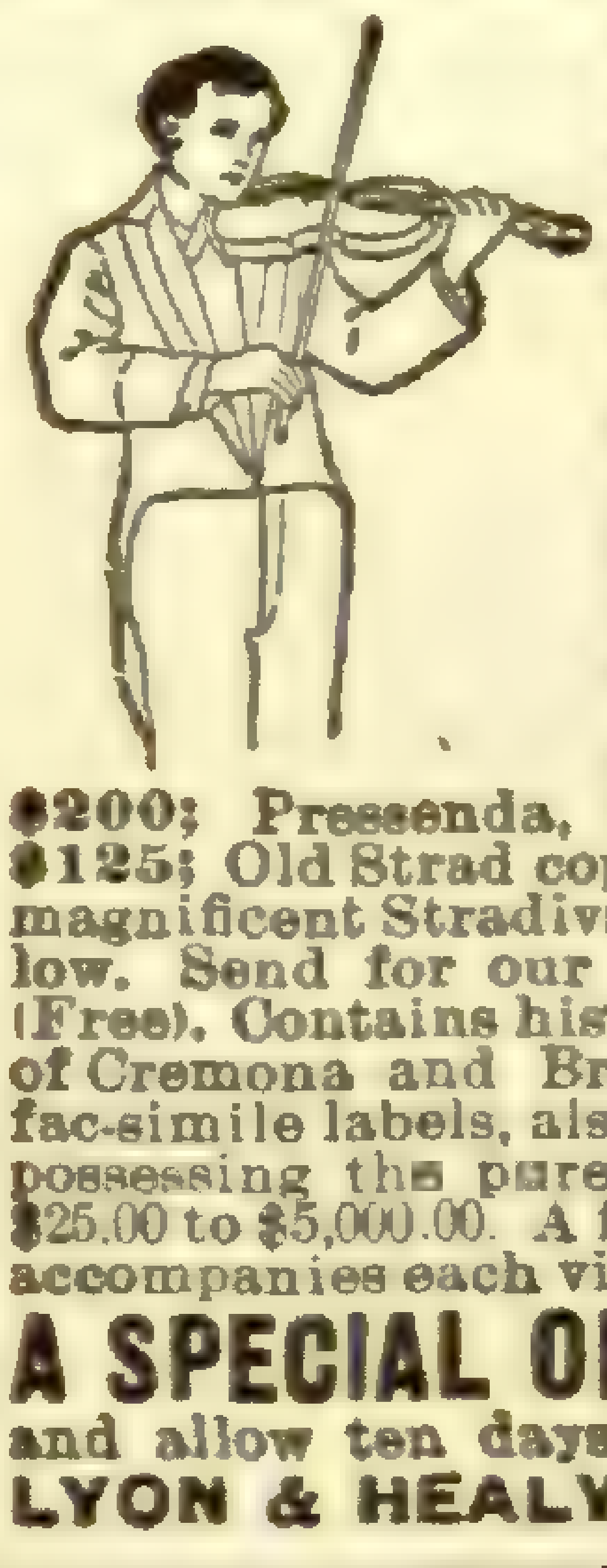

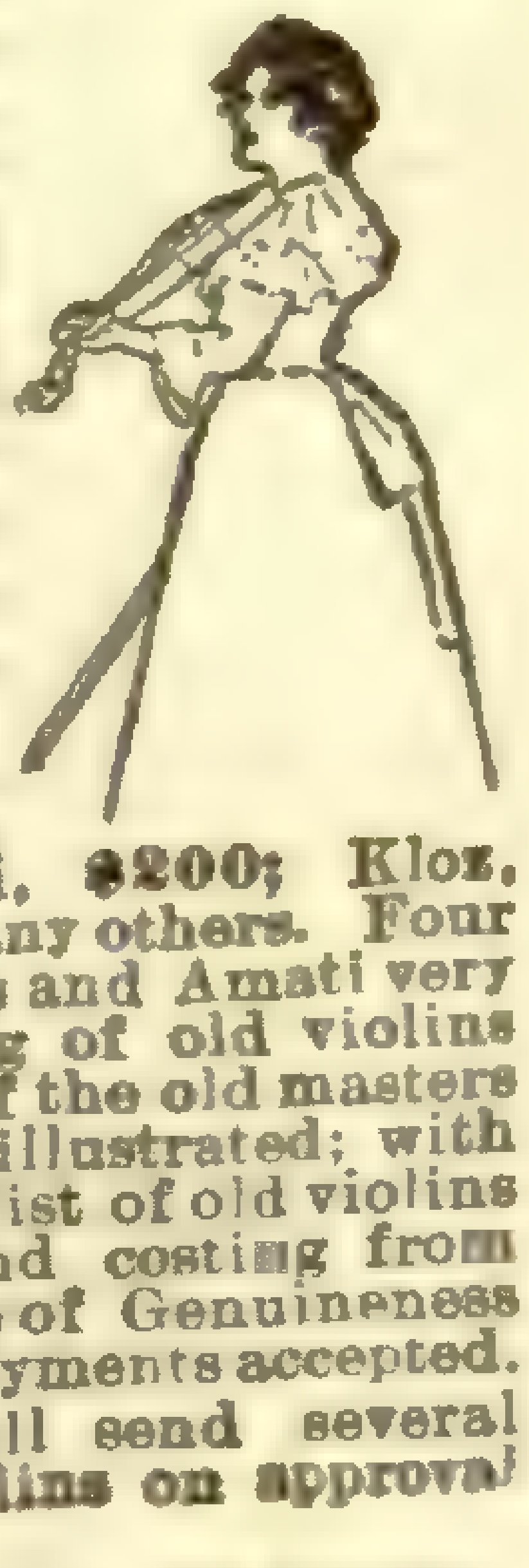

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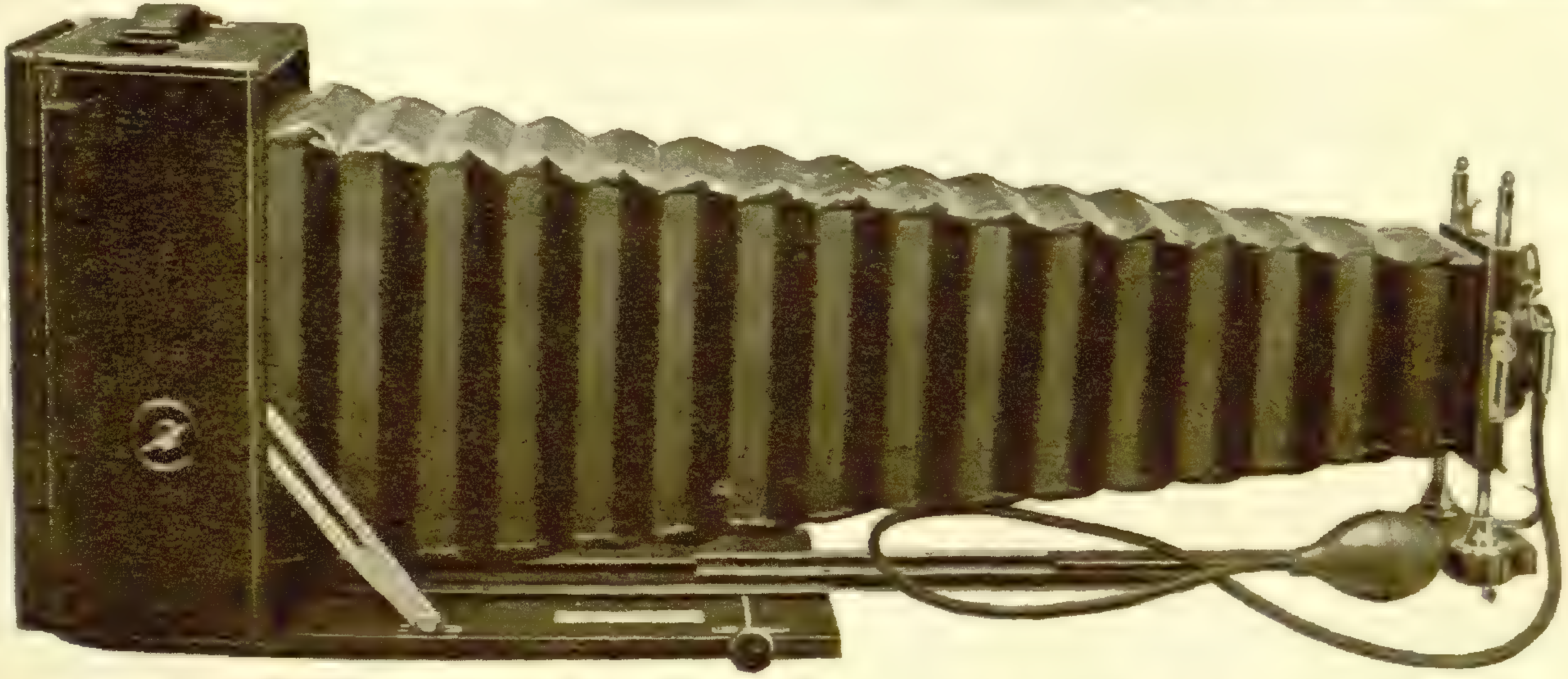

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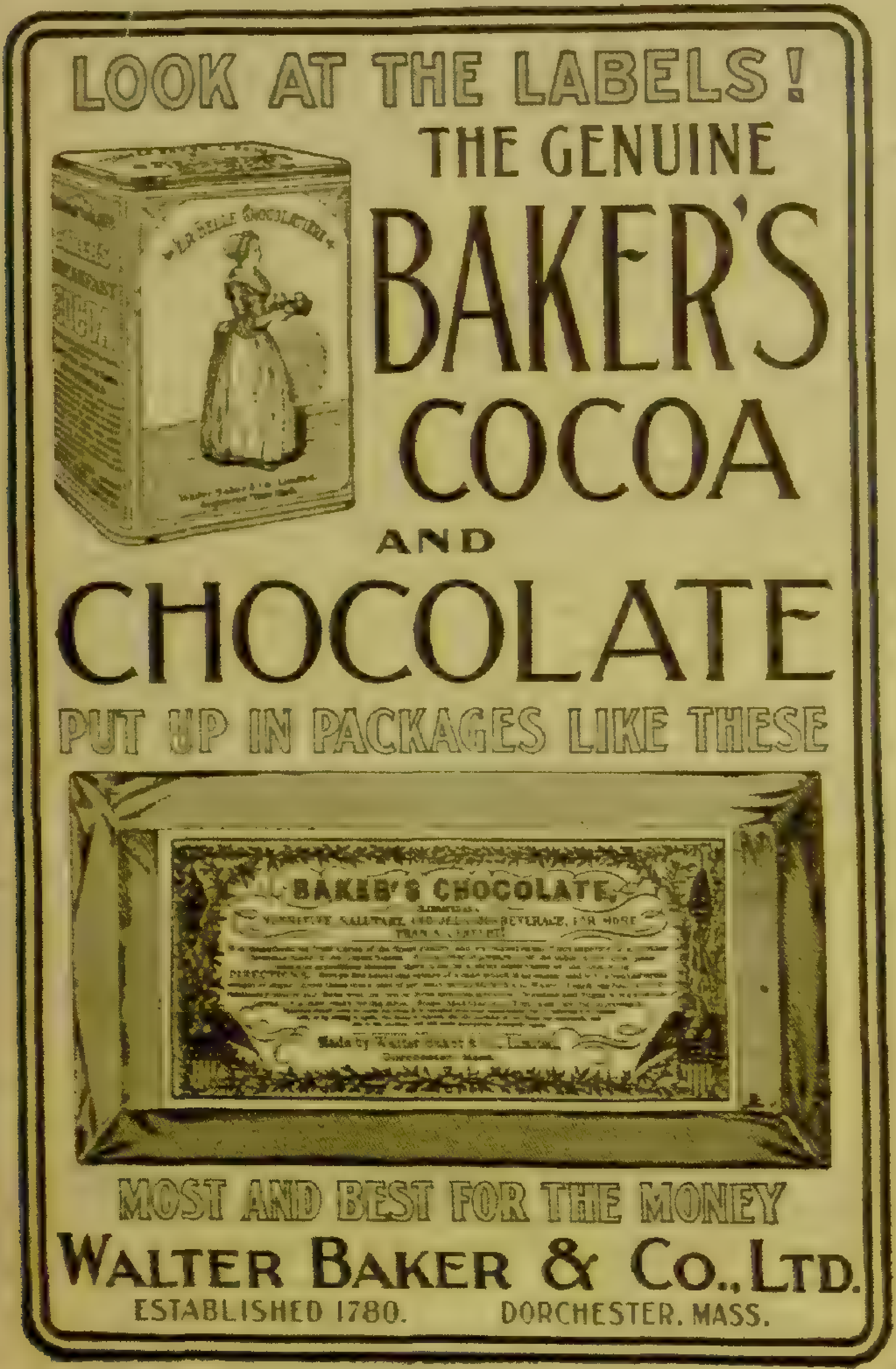

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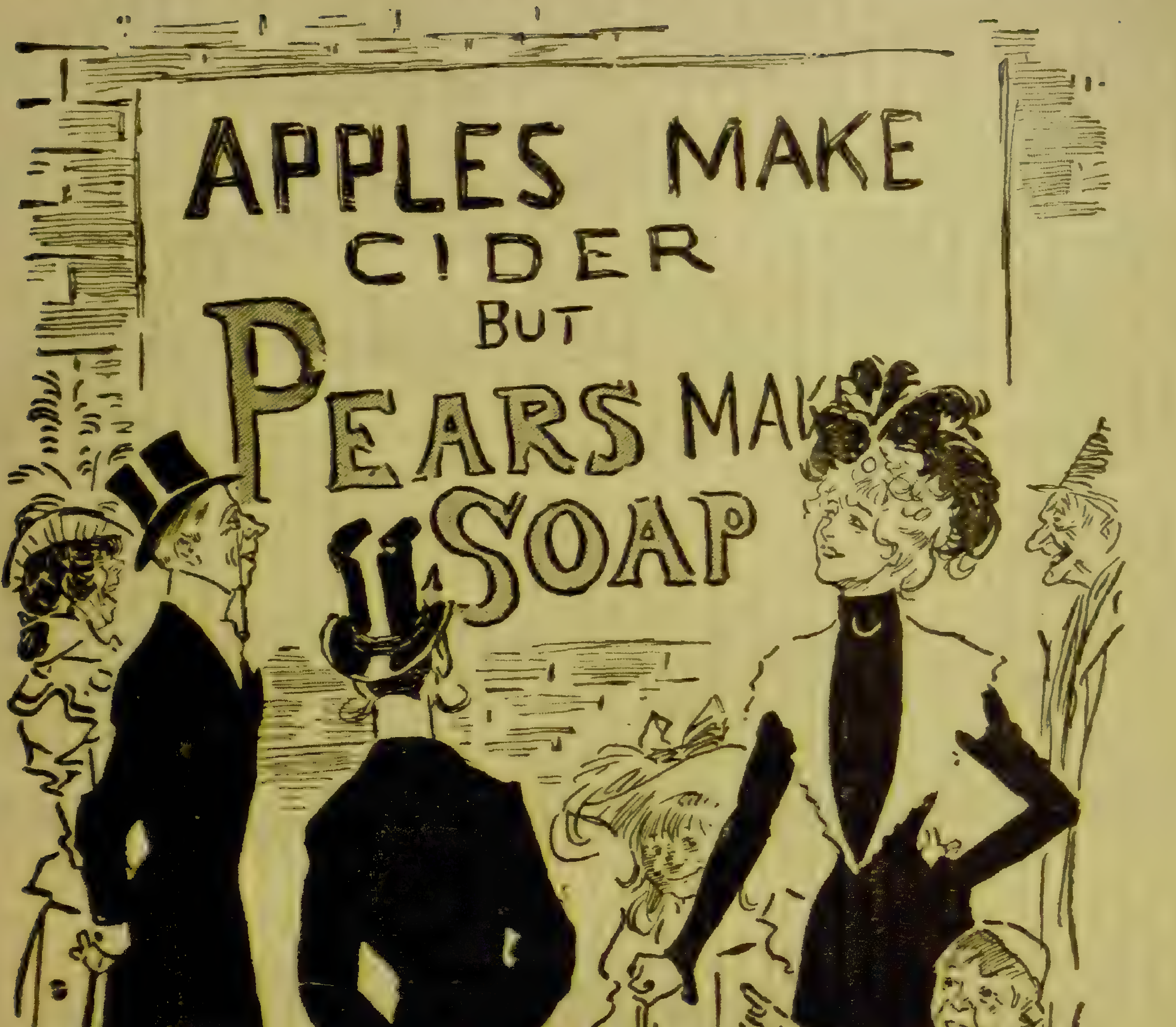
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Vol. XXXII, No. 6 **Issued December 26, 1901**

CONTENTS

THE ANATOMY OF THE OSMUNDACEAE. (WITH PLATES XIV–XVII) *J. H. Faull* - 381

BRIEFER ARTICLES.

SOME ERRONEOUS REFERENCES. *E. W. D. Holway* - 421

PUCCINIA INANIPES. *E. W. D. Holway* - 422

THE POSITION OF PLEUROCOCCUS AND MOSSES ON TREES. *Henry Kraemer* - 422

CONTRIBUTIONS TO THE KNOWLEDGE OF THE PHYSIOLOGY OF KARYOKINESIS. (WITH ONE FIGURE) *Arthur Carr Lewis* - 423

CURRENT LITERATURE.

BOOK REVIEWS - 426

BRITTON'S MANUAL

MINOR NOTICES - 427

NOTES FOR STUDENTS - 429

OPEN LETTERS.

NORMAL SOLUTIONS. *Louis Kahlenberg* and *James B. Dandeno* - 437

BASILIMA, SCHIZONOTUS, SORBARIA. *John Hendley Barnhart* - 440

NEWS - 443

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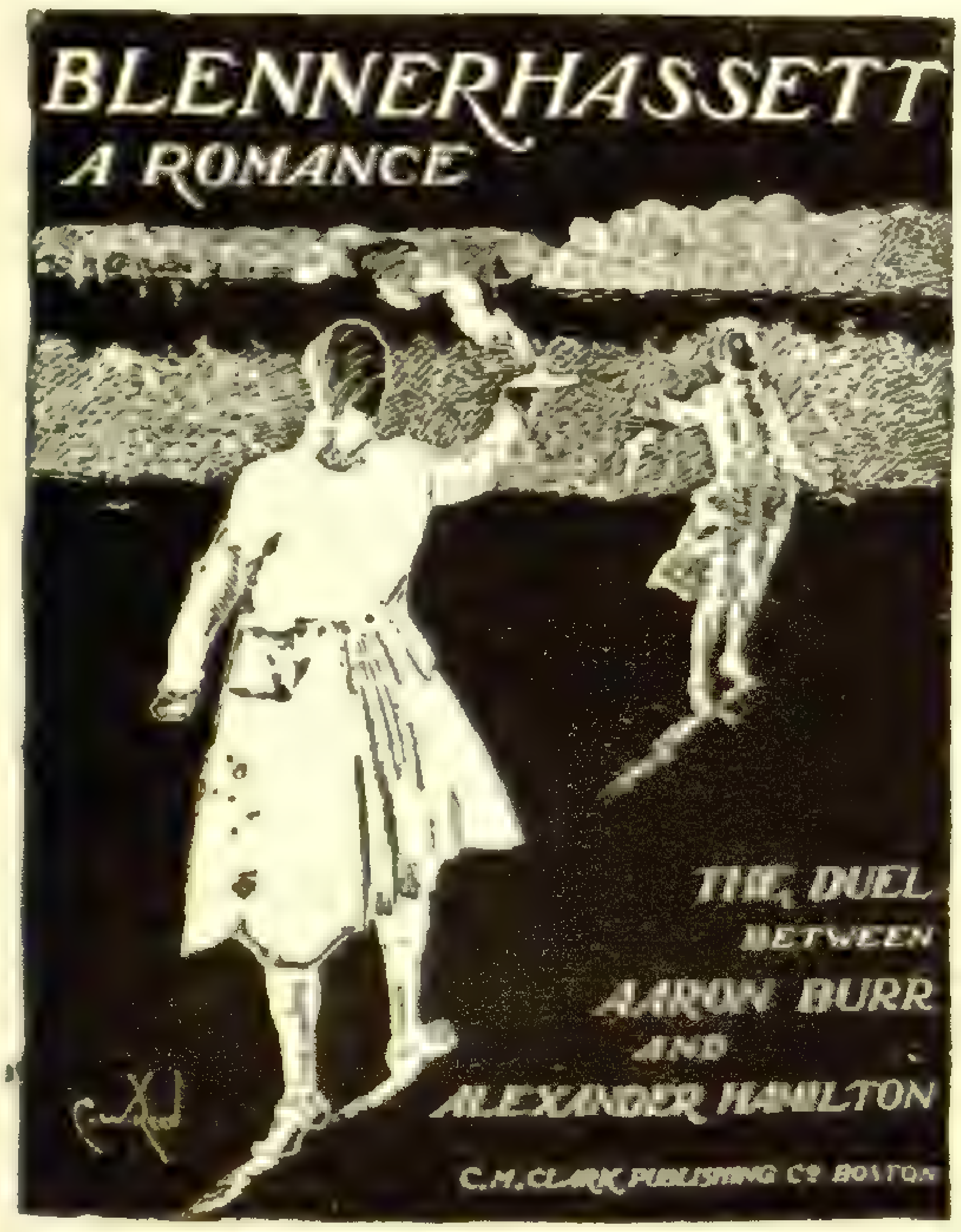
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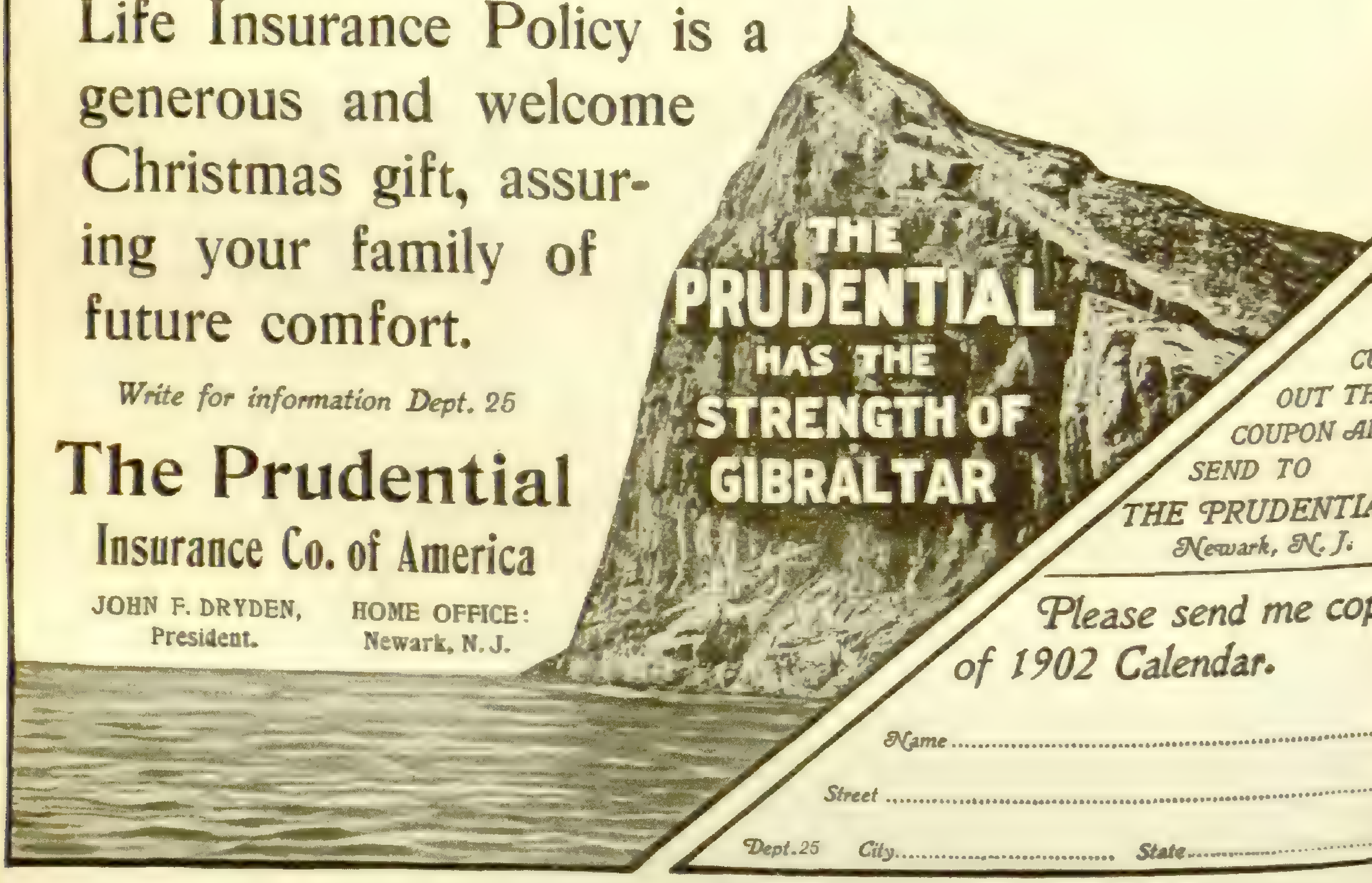
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VOLUME XXXII NUMBER 6

BOTANICAL GAZETTE

DECEMBER, 1901

THE ANATOMY OF THE OSMUNDACEAE.

J. H. FAULL.

(WITH PLATES XIV–XVII)

INTRODUCTORY.

THE cauline vascular system of the Osmundaceae has attracted considerable attention on the part of morphologists, since it is exceptional among the leptosporangiate ferns in exhibiting a type of structure presented by the phanerogams. Thus DeBary, the exponent of the "bundle system," states that "collateral bundles" are with rare exceptions characteristic of the stems and leaves of the phanerogams, but are likewise found in the Osmundaceae,[1] and that in their arrangement in the stems of the Osmundaceae they follow the "dicotyledon type."[2] Later we find Van Tieghem, the first enunciator of the "stelar theory" expressing himself as follows:[3]

> La tige des *Osmundes* et des *Todées* diffère de celle des autres Fougères. La stèle axile et sans moelle du jeune âge, au lieu de se diviser en restant grêle, demeure simple en s'élargissant progressivement à mesure que la tige grossit; elle prend une moelle de plus en plus large, à la périphérie de laquelle sont rangé en cercle un certain nombre de faisceaux libéroligneux à bois séparés, mais à libers confluents, entourés d'un péricycle commun et d'un endoderme général. En un mot la tige de ces plantes demeure monostélique à tout âge, comme celle de la plupart des Phanérogames.

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[1] DEBARY: Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne 331.

[2] DEBARY: *op. cit.* 246.

[3] VAN TIEGHEM: Traité de Botanique 1373.

Plainly enough, therefore, these eminent botanists, starting from very different conceptions, have arrived at the same conclusion, namely, that the central cylinder of the Osmundaceae resembles that of the phanerogams.

It is important to note, however, that heretofore all anatomical researches in this family have been confined to the tropical genus Todea and the cosmopolitan *Osmunda regalis;* and that hence the conclusion just stated has been based on the phenomena presented by these alone. When Van Tiegham proposed his "stelar hypothesis" several cryptogams besides the Osmundaceae were cited as exceptionally possessing medullated monostelic central cylinders. Since then more extended researches have been made which have yielded important results. Thus it has been shown that the central cylinder of Ophioglossum and of Botrychium instead of being medullated monostelic is in reality "gamodesmic;"[4] that the central cylinder in the entire family Equisetaceae, some of whose species were included in the exceptions, is of the same kind;[5] and that the central cylinder of the genus Helminthostachys is also of the "gamodesmic" type.[6] It is true that Strasburger holds[7] that the internal endodermis and endodermal sheaths about individual bundles are of intrastelar origin, and not of cortical as is the external endodermis, and that therefore these exceptions still stand; but this objection may be advantageously left for subsequent consideration. Of the apparent exceptions, the family Osmundaceae has remained untouched, and I have undertaken the present research on this anomalous case, with the primary object of furnishing data that will help determine the proper morphological interpretation of its vascular system.

The family Osmundaceae is a very limited one in point of numbers, consisting of but two genera, Osmunda with eight species, and Todea with six, and therefore constitutes a very

[4] POIRAULT: Ann. Sci. Nat. Bot. VII. **18**: 113. 1893.

[5] JEFFREY: Mem. Boston Soc. Nat. Hist. **5**: 155. 1899.

[6] FARMER: Ann. Bot. **13**: 421. 1899.

[7] STRASBURGER: Histologische Beiträge. **3**: —. 1891.

small part of the fern flora of the earth. But this does not seem to have always been the case,[8] for the Marattiaceae, although overwhelmingly predominant in the Coal period, constituted but 4 per cent. of the total filicineous flora in the Lower Jurassic, the remainder being composed of Osmundaceae and Cyatheaceae, with the related families Matonineae and Protopolypodiaceae. As to distribution, the first genus is confined to the northern hemisphere, and the Todeas are with one exception found only in Australasia. Five Osmundas belong exclusively to restricted areas in east Asia and the adjoining islands; *O. Claytoniana* occurs in the Himalayas and North America; *O. cinnamomea* in eastern Asia, North and South America; and *O. regalis* in every continent except Australasia. Of the Todeas, *T. barbara* is a native of Australia, New Zealand, and South Africa; and the remaining species, the so-called "filmy" Todeas (Leptopteris of some authors), belong to oceanic islands in the eastern south-tropical region.[9]

Of these species I have had the opportunity of studying five, namely, *O. regalis*, *O. cinnamomea*, *O. Claytoniana*, *T. barbara*, and *T. superba*. Nevertheless, in the following pages most attention will be devoted to *O. cinnamomea*, not so much because its anatomy has not previously been described, as because the writer, for reasons which will become apparent, believes it retains a more primitive type of skeletal axis than any of the family so far investigated. The material of the species of Osmunda studied was collected from several different localities, and in large quantities. Of *O. cinnamomea* specimens from fully a hundred and fifty plants were preserved and examined, and of each of the others perhaps one-third of that number. The more important points were verified from specimens taken from three different localities.

Observations have been mainly restricted to the mature root, stem, and leaf trace. Some young plants of Osmunda were studied, and the growing points of the older stems have been sectioned. But the mature stem, especially the region at which it branches, has proved to be of chief interest from the standpoint of questions of comparative anatomy.

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[8] SCOTT: Studies in fossil botany 304. 1900.

[9] DIELS: Engler and Prantl's Natürlichen Pflanzenfamilien 1^4: 377. 1900.

THE STEM.

GENERAL ANATOMY.—The mature stems are very stout rhizomes, exceptionally so in *T. barbara*, which grow in a direction somewhat oblique to the horizontal. The leaves are in a closely set tuft at the anterior end, for they are annual and the internodes are very short. The broadly winged, overlapping bases with their sclerenchymatous sheaths resist decay long after the remaining portion of the leaf has perished, and these, together with the roots, which are very numerous, greatly add to the bulk of the stem. The stem usually bifurcates once into two branches of equal size, which lie in a horizontal plane. A few specimens of *O. regalis* were found, however, in which one of the forks was much larger than the other, but the larger almost immediately divided again, so that there were three branches of about the same size lying in the same plane. The forking bears no relation to the number of leaves produced, counting from the cotyledons, nor to the age of the plant. Occasionally there is no branching at all, though maturity has long since been attained, while in rare cases it has taken place comparatively early in the life of the fern.

The rhizome exhibits a very characteristic appearance in cross-section (*fig. 1*). The outer portion, the thick external cortex (*ex. c.*), consists of very resistant, dark-brown sclerenchyma, in *O. cinnamomea* of a rich red-tinted brown, in *O. regalis* and the Todeas of a black, and in *O. Claytoniana* of a dull brown hue. The cortex is marked by leaf-traces (*lt*), which form a close spiral, and at the nodes by the escaping roots (*r*). In *O. cinnamomea* sclerification of the cortical tissue is later in taking place than in the other species. The internal cortex (*i. c.*) is parenchymatous, comparatively narrow, roughly pentagonal, and its cells are heavily loaded with starch grains. Passing the pericycle and the bast region, which form a complete sheath, the wood (x) of the stele is seen to be broken up into bundles of various shapes arranged in a circle, and separated from one another by the so-called medullary rays. These medullary rays extend out from a large pith. The pith or medulla in *O. Claytoniana* and *T. superba* is apparently homogeneous. In *O. regalis* it is often discolored and may contain one or more strands of brown sclerenchyma; in *O. cinnamomea* it is very frequently characterized by some brown sclerenchymatous tissue, and in *T. barbara* there is a large axial strand of this supporting tissue.

HISTOLOGY.—But we turn now to acquire a more intimate acquaintance with the stem as revealed by a study of its histological features. For this purpose several sets of transverse and longitudinal series were prepared, and a great many microtome sections examined. The material cut included stems of various ages. As development proceeds rather slowly, all the tissues are mature only at a considerable distance from the apex of the plant.

The cortical part of the stem has little of interest for us other than in the respects already mentioned. The sclerenchyma consists of elongated, thick walled cells, with a small lumen containing starch grains. The walls are brownish, and marked by simple pits, which are round or slit-like. According to Strasburger,[10] the endodermis is not the innermost cortical layer, but I am unable to verify this. He has made the statement that the innermost cortical layer at a certain stage divides by tangential walls to form several layers of cells; of these, the outermost becomes differentiated as the endodermis, and the remaining layers lie between this and the phloem, filling the place of a pericycle. The somewhat elongated cells of the endodermis are marked in every case by the characteristic cuticularization of the radial walls, which in transverse section shows as the "radial dot" (*fig. 6, e, e*). The "radial dot" is distinctively brought out by treatment with phloroglucin and hydrochloric acid, and also with dilute sulfuric acid. In *O.*

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[10] STRASBURGER, *op. cit.* 449.

Claytoniana the radial markings are generally not as distinct as in the rest of the species studied, and the cells are reduced in size in comparison with those of the layers in contact (*fig. 8, e*). The contents in this species, too, are meager, consisting of granular protoplasm, a nucleus which as a rule stains a deeper red with saffranin than those of surrounding cells, and a few starch granules as shown by treatment with iodin solutions. Sometimes the endodermal cells of *O. cinnamomea* are likewise apparent by the lack of contents, in contrast to the heavily-laden cells, both ectad and centrad. Generally in this species, as in the remaining ones, *T. superba* excepted, the cells are filled with tannin, so that the endodermis stands out very distinctly.

The pericycle is entirely parenchymatous and consists of several layers—in *O. Claytoniana* and Todea of two or three, in *O. cinnamomea* of three or four, and in *O. regalis* of one to three. The cells are elongated, cylindrical, provided with large nuclei, and filled with finely granular contents, part of which is starch. Haematoxylin imparts to this tissue a light blue color. Tangential sections show that the orientation of the cells is very irregular (*figs. 3* and *9, p*). Immediately opposite the point of origin of a leaf trace, and for a short distance below, the long axes of the cells run parallel with the long axis of the stem, but for the most part in the remaining regions of the stem there is considerable disturbance, though only in tangential planes. This disturbance is commonly so marked that the long axis of the cell is at right angles to the stem axis, and between this and the parallel position there is every gradation. Therefore in transverse section these cells are either round or more or less tangentially lengthened (*fig. 8, p*). This variation in orientation is of interest, as it is connected with a similar phenomenon in layers lying nearer the cauline axis, namely in the phloem region.

XYLEM.—Before dealing with the phloem, however, it will be convenient to describe the xylem. The wood elements are of two kinds, namely, small ringed and spiral elements constituting the protoxylem, and scalariform tracheids which are of later development constituting the metaxylem. Occasionally a parenchymatous cell is found among the tracheids. A transverse section shows, as mentioned before, a ring of variously shaped bundles; and by tracing these up and down, or by boiling a piece of stem in potash and then removing the softer tissues, there is shown to be a network forming the wall of a hollow cylinder, the strands being the "bundles" of DeBary, and the meshes the spaces occupied by the "medullary rays." Though there is a great deal of regularity in the apparent construction of this network, as proved by DeBary and Zenetti in *O. regalis*, yet a study of development shows that the "bundle theory" is inadequate for giving the right conception of the vascular system. In the young stem of the Osmundaceae the wood forms a completely closed cylinder, and Van Tieghem, basing his conclusions on Todea and *O. regalis*, has stated this to be the case for the whole family. I am able to state that the phenomena in the young stem of *O. cinnamomea* and *O. Claytoniana* are in accordance with his general conclusions in this respect.

Now directly above the point at which a leaf trace leaves the stele the wood is not developed for some distance. This gap is filled by parenchyma chiefly, except at the outer part, which is occupied by sieve tubes. There are exceptions in *O. cinnamomea* to be described later. Thus a transverse section of the stele, just above a node, shows a ring of wood broken at one place, the break being occupied by the tissues just referred to; in other words, the stele here has one medullary ray. *Fig. 23* shows a transverse section of the stem of *O. Claytoniana* through this region. Still further up the internode the ring is complete again. There is the same sort of gap above the second node. However, as the nodes become more frequent, that is, as the internodes become shorter, a leaf gap extends through more than one internode, and in a transverse section there is more than one medullary ray, until in the full grown stem, where a leaf gap extends through several internodes, a transverse section shows several gaps cut across, or in other words shows several medullary rays. It is therefore evident that the number of medullary rays seen in any transverse section depends on the frequency of the nodes and the length of the gaps. In well nourished stems the number is greatest in *O. Claytoniana* (*fig. 17*), there usually being about twenty, and in *T. barbara* (*fig. 24*) the fewest. In this species the gaps are quite short, so that while the wall may be thin in many places at any given level, there are not more than two to six medullary rays seen in the cross section (*fig. 24*).

The persistent portions of the cylinder of wood, the "bundles," present various contours in cross section, the shape of any particular portion lying between two adjacent gaps, that is, of any strand, varying with the level at which it is cut. Just below where the leaf trace is given off, the wall is hollowed out on the side towards the pith, so that the transverse section of the strand presents a horseshoe shape (*fig. 17*). The middle of the inner surface of the strand at this level is occupied by protoxylem, which consists of about a half dozen small ringed and spiral vessels. Following the strand down, it is seen that the arms of the horseshoe thicken on the sides facing one another, especially towards the ends of the arms (*fig. 15, s*). Finally, the opening between the ends is fully closed and a small group of parenchymatous cells lying exactly centrad of the protoxylem is thereby enclosed (*fig. 17, s*). The parenchyma is more and more encroached upon by the xylem, until lower down it is seen no more. Not far below where the parenchyma vanishes, the protoxylem in that strand likewise disappears. Somewhat above the level at which the parenchyma is enclosed the strand begins to thin out on the outer side, a sharp trough-like indentation appearing, but not in the same radius as that in which the protoxylem lies. This trough continues to deepen until a few nodes down the strand is cut through, the point at which the break occurs being, indeed, the apex of a leaf gap. Thus neither the outer nor the inner surface of the cylinder of xylem is smooth; the lower part of a leaf gap can be traced as a hollow on the inner surface just below where the leaf is given off, ending as a blind tube amongst the tracheids, while the upper end of the gap may be traced as a furrow on the outer surface of the cylinder, gradually becoming more and more shallow

The protoxylem occurs in small groups of six to eight cells each, and a transverse section of the central cylinder shows from five to seven of these groups. Each group of protoxylem elements passes out in its entirety into a leaf trace, and on following back from the leaf trace each vanishes as already described. The protoxylem is therefore not continuous throughout the stem, but is in small, discontinuous strands. This fact has been recorded for *O. regalis* by Zenetti.[11]

Lying externally to the wood are from four to six layers of elongated parenchymatous cells, rich in protoplasmic contents and in small starch grains. They are continuous with the parenchymatous cells of the medullary rays and do not materially differ from them. Those occupying the middle of the medullary rays have more meager contents, and towards the stem axis they become larger. That there is a "xylem sheath" characterized by cells of greater size and richer contents such as Zenetti describes for *O. regalis*, I cannot affirm, and certainly there is not such a sheath in *O. Claytoniana*.

PHLOEM.—The tissues that have just been described are bordered by the phloem, which consists chiefly of sieve tubes. Parenchymatous cells are sometimes met with in isolated positions in the metaphloem, and between the metaphloem and the protophloem they constitute a more or less broken layer, most pronounced in *O. Claytoniana*, and least constant in *O. regalis* and *T. barbara*. The sieve tubes are strongly developed and are of the "type vigne" of Lecomte. They are large, have thin walls of unmodified cellulose lined with a delicate layer of protoplasm, and are devoid of nuclei. They are provided with oblique terminal walls and are furnished with sieve plates both simple and compound. The sieve plates are covered with "globules brillants," and by treatment with proper reagents callus plugs may be demonstrated in them. The sieve tubes of the protophloem are smaller than those of the metaphloem and their terminal walls are not as oblique.

As there has been considerable difference of opinion regarding the disposition of the phloem in *O. regalis*, it will be well to define a sieve tube. Both Russow and Janczewski have studied sieve tubes very carefully, and Poirault has more recently reinvestigated the subject in the vascular cryptograms. The investigator last named summed up his observations on sieve tubes in the roots of vascular cryptogams in the following terms :[12]

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[11] ZENETTI: Das Leitungssystem im Stamm von *O. regalis*. Bot. Zeit. 53:63. 1895.

> Les tubes criblés peuvent se rapporter à deux types : le premier caractérisé par des cloisons transverses perpendiculaires aux faces principales et ne portant qu'un seul crible (*type Courge*, Lecomte) ; le second reconnaissable à ses cloisons transverses très obliques portant d'autant plus de cribles que leur obliquité est plus grande (*type Vigne*, Lecomte). On trouve, en outre, sur les faces longitudinales des ponctuations isolées ou réunies en très petits groupes, constituant rarement des cribles aussi développés que ceux des faces transverses. Le contenu de ces tubes est un liquide hyalin tenant en suspension de nombreuses sphérules réfringentes, rassemblés surtout au niveau des cribles et des ponctuations isolées. Il n'y a pas de noyau. La membrane est cellulosique.

He further adds that two substances occur as a rule — (1) the "globules brillants" already mentioned, and (2) "les *bouchons calleux* qui font corps avec la membrane et peut-être la traversent entièrement."

In dealing with the sieve tubes of the stem and petiole he does not point out any other peculiarities, but deals at length with the callus plugs, and the perforation of the sieve plates.[13] The observations of Russow, Janczewski, and Poirault agree for the most part, except in reference to the callus plugs.

The following criteria would seem to be distinctive in determining the presence of sieve tubes in the Osmundaceae ; the existence of sieve plates, the absence of nuclei, and the presence of "globules brillants." Less distinctive and rather as a confirmatory test I have sought for callus. Russow made this test one of paramount importance, but it seems best in dealing with the vascular cryptogams to give it a second place, and for the following reasons : (1) the callus, so-called, in the seive tubes of the vascular cryptogams may not be identical with that found in phanerogams; (2) it occurs in minute quantities only, and in some plants (*e. g.*, the Ophioglossaceae) probably does not occur at all; (3) its presence is determined by delicate microchemical means, and then only by limited color reactions.

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[12] POIRAULT : Récherches sur les cryptogames vasculaires. Ann. Sci. Nat. Bot. VII. **18** : 138. 1893.

[13] POIRAULT : *op. cit.* 191.

Janczewski[14] claimed to have found callus in *Pteris aquilina* alone of all the vascular cryptogams he examined, and states that it does not occur in *O. regalis.* The reagents he used were Schulze's solution (or chlor-zinc-iodin) and rosolic acid. On the other hand, Russow found callus in all of the sieve tubes he examined. The reagent he used was a mixture in variable proportions of chlor-zinc-iodin and potassium iodid-iodin. It should be stated that in the vascular cryptogams callus occurs in the wall of the sieve plate, appearing as if it were a part of the wall. After staining with a suitable iodin solution, the callus shows in face view as one or more round brown spots, and in section as rods or granules occupying the entire thickness of the lamella. Poirault has largely corroborated Russow's observations. He disagreed with Russow's generalization that it is a constant feature of sieve tubes, for he states that he has been unable to find any trace of callus in Angiopteris and Ophioglossum.[15] In view of these investigations, therefore, it becomes a matter of interest to know if the sieve tubes of Osmundaceae show the phenomena of callus as described by Janczewski for Pteris, and by Russow and Poirault for many others of the vascular cryptogams.

Accordingly tangential and transverse sections about five microns thick, of the three Osmundas studied and of *T. barbara* were cut from mature pieces of stem embedded in celloidin. In the present research the writer has tried several stains, such as ruthenium oxid, Hofmann's blue, rosolic acid, and Russow's mixture. These have been applied to sieve tubes of plants from widely separated groups, such as Vitis (summer and winter sieve tubes), Tilia, Pinus, Pteris, and the mixture of chlor-zinc-iodin and potassium iodid-iodin proved to be by far the most satisfactory reagent for the demonstration of callus. The two constituents of this reagent were prepared fresh, and then mixed in different proportions until one giving the best results was obtained. The proportions vary with the different kinds of plants tested. In using this stain, though the presence of the celloidin is not a serious objection, it is preferable to dissolve out the celloidin, wash in alcohol, then in distilled water, and examine in stain on the slide.

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[14] JANCZEWSKI: Tubes cribreux. Ann. Sci. Nat. Bot. VI. 14:50. 1882.

[15] POIRAULT: *op. cit.* 192.

In face view it is difficult to make observations on account of the "globules brillants," hence the most reliable observations can be made on sectioned plates. Almost at once after applying the stain, the callus plugs become evident, staining a dark red-brown (*fig. 7*). They appear as more or less fine rods, completely traversing the sieve plate, and their number in a sieve plate depends on its size. The cellulose is slower in staining; at first it is light blue or a violet, and later a deep blue. Hence the callus plugs are to be seen most clearly in the early stages of the staining process. The stain unfortunately is not permanent. Callus was clearly demonstrated in the species under investigation, but on account of the size of the cells and of the sieve plates, *T. barbara* proved the best subject for the purpose. As one of the characters of the sieve tubes of the Osmundaceae, we record, therefore, the regular occurrence of callus plugs in the sieve plates.

The "globules brillants" are exceedingly abundant in the sieve tubes, and especially in the older ones (*fig. 7*). While they adhere to the protoplasm of the cell and may be found in any part of the cell they are by far most abundant about the sieve plates, dotting their surface, filling the pits, and surrounding the entrance to the pits. They are evidently not homogeneous, but appear to consist of two substances, one of which is more refractive than the other, for by slight focusing up and down they change from a dark looking, opaque granule to a light semi-translucent spherule. Iodin solutions stain them brown, not appreciably different from the callus plugs. Occasionally irregular fragments of matter are found in the cell, which also stain a similar brown. The relation between these fragments, the "globules brillants," the callus, and the disappearance of the nuclei calls for further investigation.

The sieve plates are very numerous, and vary in size and form. The walls of the pits are abrupt, and the number of pits varies with the size of the plate. The larger plates are irregularly oblong and the smaller ones are round. In Todea they are largest and most numerous. Having described the sieve tubes at some length, we shall now examine their distribution.

The phloem forms a continuous sheath, the outer portion of which is the protophloem. To this peripheral part of the phloem I find that DeBary and Zenetti alone make specific reference. The former states[16] that this region of the central cylinder is characterized by "quergestreckte Zellen," but he offers no opinion as to the nature of the tissue in question. Zenetti divides the zone into strands of typical protophloem and connecting portions of "quergestreckte Zellen." The typical protophloem is in short strands one cell thick, lying ectad of strands of xylem which are about to give off the leaf traces. The "quergestreckte Zellen" he cannot recognize as sieve tissue, because of the "quergestreckt" form and the position of the cells. This tissue in *Osmunda regalis*, consequently, forms a cylinder interrupted by the strands of protophloem only, but Zenetti found it to be generally two cells in thickness and opposite the medullary rays often several cells deep.

I have ascertained that the "quergestreckte Zellen" are devoid of nuclei; their walls are of cellulose, staining violet or blue with iodin solutions. They are rounded, elongated elements, with more or less oblique terminal walls; and are characterized by the possession of sieve plates which show the callus reaction when treated with Russow's reagent; the cells contain an abundance of "globules brillants" which are aggregated especially about the plates; the protoplasm is reduced to a thin parietal layer. The characters of the typical protophloem cells are the same as those of the "quergestreckte Zellen" except in regard to orientation (*fig. 6*).

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[16] DEBARY: *op. cit.* 360.

Transverse sections show that the long axes of the so-called "quergestreckte Zellen" are tangentially placed, and never radially to any degree. To determine the slant of the long axes, therefore, with reference to the axis of the stem, tangential sections must be made. If such be examined it is seen that some are exactly at right angles to the axis, others are almost or entirely parallel, and between these extremes there is every gradation. This at once explains the difference in "width" of the "quergestreckte Zellen" in transverse section. It is further to be noted from the tangential sections that the ends of typical protophloem cells never abut against the long sides of the "quergestreckte Zellen," but there is a gradual change in the direction of the latter so that their ends communicate with the protophloem and it is quite impossible to say where the typical protophloem ends and the "quergestreckte Zellen" begin.

The root and leaf have been examined for "quergestreckte Zellen," for if these elements constitute a characteristic textural feature of the Osmundaceae they would naturally occur elsewhere than in the stem. They are not present at all in the appendicular organs. Further, in the young sporophyte, where the leaf gaps are far apart, they are absent from considerable portions of the stem. The real nature of the "quergestreckte Zellen" will be discussed after observations on their development and their relation to the leaf traces have been described.

The "quergestreckte Zellen" and the typical protophloem cells form a continuous sheath in all the species studied. In *O. Claytoniana* the elements of this sheath are very much smaller, and so it is easier to distinguish them from the metaphloem. In *T. barbara* their histological characters are best studied because of their relatively large size. Frequently in *O. cinnamomea* and *O. regalis* it is difficult to decide in the mature stem whether or not certain cells belong to this sheath or to the metaphloem. But evidently in all of the species the sheath is rarely more than two cells in thickness, and often, especially in

O. Claytoniana, there is but a single layer. Opposite outgoing leaf traces the sheath is reduced to a single stratum.

The *metaphloem* forms a hollow cylinder consisting of large sieve tubes such as have already been described. They are thin-walled, and especially in *O. regalis* in the older parts of the stem have often collapsed. The sheath is one or two cells thick opposite the strands of xylem, and several cells in thickness opposite the medullary rays (*fig. 8, ph*). Most of the tubes run parallel with the long axis of the stem, but here and there "quergestreckte" examples occur.

This cylinder of metaphloem has a smooth outer surface, but the inner surface is rendered very uneven on account of the wedge-like proliferations of the sieve tissue opposite the leaf gaps. Since this is a phenomenon common to all the species studied, we naturally seek an explanation of this peculiar disposition of the phloem. In his memoir on sieve tubes Janczewski,[17] who could hardly have been prejudiced by any stelar theories, noted that isolated sieve tubes occur occasionally here and there in the medullary rays of *O. regalis*. The writer has found undoubted cases of the same thing in *O. cinnamomea*.

Two such eminent botanists as DeBary and Strasburger have disagreed as to the topographical distribution of the layer of metaphloem sieve tubes in *O. regalis*. The former states[18] that the sheath is continuous, while the latter states[19] that he puts himself in opposition to DeBary on this point, for he considers the phloem to be interrupted opposite the medullary rays. Strasburger does not say for what reason he considers the cells opposite the medullary rays not to be sieve tubes. My own observations on *O. regalis* are precisely in accord with those of DeBary and Janczewski. The cells opposite the medullary rays differ in no way from the sieve tubes opposite the xylem strands. I have found the same to be true of the other species studied, with the additional observation that isolated sieve tubes occur sometimes in the tissues filling the leaf gaps of *O. cinnamomea*.

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[17] JANCZEWSKI: *op. cit.* 66.

[18] DEBARY: *op. cit.* 360.

[19] STRASBURGER: *op. cit.* 449.

To this last observation I have two others to add, namely, the occurrence of an internal phloem in which the sieve tubes form a more or less continuous ring (*figs. 21*, and *22*), and in rare cases the union of external and internal phloem through a leaf gap. In a certain rich, moist situation about a dozen well nourished plants of *O. cinnamomea* grew, of which, on examination, five showed the phenomenon of a continuous layer of internal phloem. Search in an adjoining locality resulted in finding specimens which showed the same feature. To extend the range of observations, I visited a peat bog some twenty miles distant from Toronto, where I knew the cinnamon fern grew, and secured specimens characterized by the same peculiarity. *Fig. 21* shows a transverse section of a stem found in this last locality. The sieve tubes of this internal phloem are as typical as those of the external, and except for their position not be distinguished from them. They do not always form a continuous ring as do the sieve tubes of the external phloem, but are often in more or less detached groups, embedded in small celled parenchyma. The layer of sieve tubes is from one to three cells thick. It should be added that internal phloem occurs only near where the forking of the stem takes place.

O. cinnamomea shows likewise two other features which are constant throughout every part of the stem, and at once distinguish it from other species: (1) an internal endodermis, and (2) several layers of parenchyma between this and the xylem.

INTERNAL ENDODERMIS.—The internal endodermis possesses the characteristic radial dot, though sometimes not as clearly distinguishable as in the external endodermis (*i. e.*, *fig. 2*). Its cells are usually larger than those of the latter, but are filled with similar contents, most frequently tannin (*fig. 15*). It is further to be noted that it bends outwards opposite the leaf gaps (*figs 10*, etc.), and not infrequently connects through them with the external endodermis. I have examined scores of stems of the cinnamon fern, and in every specimen there was an internal endodermis. On the contrary, it seems to be invariably absent from the other species studied. As the central cylinder of the family Osmundaceae has heretofore been classed as monostelic, the existence of an internal endodermis in one of the species is therefore a matter of considerable moment, especially if it be regarded as a real phloeoterma.

Between the internal endodermis and the xylem there is a cylinder of elongated parenchyma, rich in starch and protoplasm, and from two to seven cells in thickness. This layer is continuous with the medullary rays. In *O. regalis, O. Claytoniana, T. barbara*, and *T. superba* a similar but thinner layer it found as a rule, and the cells are always smaller and richer in contents than those of the medulla on which they border.

THE MEDULLA.—The medulla is very large in this family, particularly so in *O. Claytoniana*, and consists of large-celled parenchyma. Most of the cells are partly filled with large starch granules, but frequently some of them contain tannin, especially in *T. barbara*. A brownish fluid may occur in intercellular spaces, and in *O. regalis* within the cells themselves. In these regards there is often a striking resemblance between the parenchyma of the medulla and that of the internal cortex in the same plant. But there yet remains to be described a still more significant phenomenon, namely, the occurrence in the pith of brown sclerenchyma of the same kind as is found in the external cortex (*figs. 14* and *20*). This is probably a primitive feature, and in this, as in many other respects, *O. cinnamomea* proves to be most interesting. Out of forty-four pieces of stem, chosen at random, and representing a corresponding number of different plants of this species, twenty-five of the examples showed brown sclerenchyma in one or both ends. It occurs as a central strand, varying in size from a few cells to almost the limits of the pith, or as several small strands irregularly arranged. *Fig. 14* is a photograph of the transverse section of a stem in which there is a large axile strand, and *fig. 15* of one in which the sclerenchyma is entirely absent from the pith. Further it has the peculiar habit of being present at one level, but perhaps not at another; so it is likely to be found in nearly every plant if the stem be sectioned from end to end.

This same habit is characteristic of its appearance in *O. regalis* (*fig. 20*), but more often it is not present at all. That brown sclerenchyma occurred in the pith of *O. regalis* did not escape the observant DeBary,[20] but elsewhere I find no reference to this fact. Strangely enough, however, out of thirty-five or forty plants harvested from one locality there was not a trace of sclerenchyma to be found in the medulla of any of them, while in one region not far distant 25 per cent. showed this phenomenon, and in another a still higher per cent.

Parenchyma is the sole constituent of the medulla of *O. Claytoniana* (*fig. 17*). This is probably true of *T. superba* too. *Fig. 25* is a cross section of *T. barbara* taken too near the growing point to show sclerenchyma, but farther down the medulla was occupied by a large strand of this tissue (*fig. 24*).

Thus medullary brown sclerenchyma is usually present in *O. cinnamomea*, in *O. regalis* not uncommonly, and in *O. Claytoniana* not at all. In *T. barbara* it also occurs, but apparently not in *T. superba*. It is perhaps significant that such series can be arranged, but of greater importance is the fact that the occurrence in the Osmundaceae of brown sclerenchymatous tissue, apparently within the cauline central cylinder, has no parallel among existing ferns.

THE FORK.—There yet remains to be described the anatomy of one particular portion of the stem, the part in the region of bifurcation. It has been stated that it is peculiar to the stem of the Osmundaceae to fork once, and that in a horizontal plane. We shall treat first of the phenomenon in *O. cinnamomea*. Tracing the main stem forwards, it is seen to become flattened and then to become constricted in a median vertical plane. Immediately anterior to the point of bifurcation of the vascular axis, there is a wide ramular gap in the central cylinder of each branch (*fig. 10*). Sections of the main axis immediately below the fork show two bands of phloem, one on the upper and one on the lower internal surface of the central cylinder (*fig. 13*). Sections passing through just in front of the region of bifurcation show similar bands of phloem along the inner wall of the central cylinder of each branch (*fig. 11*). Cases have been described above, in which there is a complete cylinder of internal phloem instead of the two isolated bands just referred to (*fig. 21*). The internal and external phloem connect through the ramular gaps (*fig. 11*). Likewise the internal and external endodermis are in textural continuity through these gaps, so that there is free communication between the cortex and the pith (*fig. 10*).

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[20] DEBARY: *op. cit.* p. 290.

Sometimes the cortex lying between the two branches contains brown sclerenchyma which is continuous through the ramular gaps with strands of the same tissue occurring in the medulla of the branches. Frequently in less vigorous plants a transverse section of the main axis posterior to the point of ramification shows a diamond-shaped piece of cortex surrounded by endodermis (*fig. 12*). Posteriorly this included piece of cortex becomes continuous with the medulla of the main axis (*fig. 13*), and anteriorly with the general cortex (*fig. 11*).

Twenty-five forks of *O. cinnamomea* were selected at random and sectioned. Twelve of them presented the phenomenon of typical wide ramular gaps. Six of them were of the reduced kind just described. In five cases there were gaps in the xylem only, cortex and medulla never becoming continuous; and in two even the xylem did not open up (*fig. 16*). For reasons to be outlined later, the writer believes the wide gaps to be the most primitive.

O. regalis presents a much degenerated form of ramular gap, for here only the xylem opens (*fig. 19*). In *O. Claytoniana* the degeneration is carried still farther, for as a rule there are no branch-gaps at all (*fig. 18*). In *T. barbara* the xylem alone may open up.

The phenomena of the fork may be thus summarized:

(1) Complete ramular gaps occur only in *O. cinnamomea.*

(2) Internal phloem occurs only in *O. cinnamomea.* It is found in the branches just above, and in the parent axis just below the point of bifurcation of the central cylinder.

(3) The internal phloem may form an entire cylinder.

(4) Where gaps are complete, the cortical and medullary tissues connect through them.

(5) Thus sclerenchyma of the cortex is sometimes continuous with sclerenchyma in the medulla of the main axis, and of the branches.

(6) *O. cinnamomea* presents the following forms of ramular gaps arranged in order of degeneration, (*a*) complete gaps, (*b*), phloem and xylem only open, (*c*) the xylem alone opens, (*d*) no gaps at all.

(7) *O. regalis* and *T. barbara* show gaps in the xylem only, and in *O. Claytoniana* there are usually none at all. *O. Claytoniana*, therefore, presents the extreme case of degeneration.

THE LEAF TRACE.

The leaf traces pass very obliquely up through the external cortex. A section of a leaf trace shortly before it passes into the petiole presents some noteworthy characters. In the first place there is no pith, but a solid horseshoe-shaped mass of xylem with the convex side turned outwards (*fig. 5, x*). The xylem is made up of large scalariform tracheids with a protruding mass of a few small vessels constituting the protoxylem. The protoxylem is situated on the inner face of the single strand of xylem (*px*), and is continuous with that of the stem. In *T. barbara* it frequently breaks into two or three groups.

Surrounding the wood is a layer of parenchyma, which on the concave side of the xylem quite fills the space between the arms of the horseshoe. The phloem consists of a crescentic band of sieve tubes, one to three cells thick on the external side of the leaf trace (*ph*), and a smaller band on the opposite side (*ph*). The protophloem consists of small elements which form a ring, broken only on the concave side of the xylem. Here the ring is completed, however, by the inner band of metaphloem. In *O. cinnamomea* and *T. barbara* isolated protophloem cells have been observed by the writer on the side of the inner band of metaphloem towards the stem axis. On the convex side the protophloem is separated from the metaphloem by parenchyma. There are no "quergestreckte Zellen." The pericycle consists of two or three layers of cells, and is bounded by a well developed endodermis continuous with that of the stem. With reference to the attachment of the leaf trace to the cauline vascular axis Zenetti has given a very careful and accurate description.[21]

Strasburger has held[22] that the stele of the petiole of *O. regalis* is a collateral bundle. He has considered the inner band of metaphloem to be a parenchymatous tissue. However, the cells of this band prove to be characteristic sieve tubes, and are continuous with sieve tubes in the stem opposite the medullary rays. The leaf traces, therefore, are undoubtedly concentric. Several botanists have arrived at the same conclusion for *O. regalis*.[23, 24]

In summary, the most important features of the leaf trace are: (1) the absence of a pith, (2) the endarch xylem strand. (3) the concentric type of stele, (4) the absence of "quergestreckte Zellen," and (5) the cylinder of protophloem completed on the inner face by a band of metaphloem.

THE ROOT.

The roots have a definite relation to the leaves, both in position and in numbers. Two roots invariably originate from the base of every leaf trace, or from the central cylinder immediately below. They come off at the same level, one opposite each arm of the horseshoe-shaped strand of xylem (*fig. 18*) in every case where there are just two roots to a leaf. They grow almost directly outwards, and so in a transverse section of the stem are cut longitudinally. In such a section it is seen, likewise, that the cortical tissues of the stem and root are entirely independent of each other, and that, therefore, the root is of endogenous origin. This fact is true of the secondary roots also.

[21] ZENETTI: *op. cit.* 69.

[22] STRASBURGER: *op. cit.* 448.

[23] SCOTT: *op. cit.* 319.

[24] ZENETTI: *op. cit.* 66.

The cortex is exceedingly thick, forming by far the main bulk of the root, and consists of large celled sclerenchymatous tissue. The cortical cells diminish in size towards the periphery, and become thicker walled. In *T. barbara*, however, there is a discontinuous ring of exceedingly thick walled brown sclerenchymatous cells immediately surrounding the vascular axis. The endodermis, which is continuous with that of the stem and leaf, is very pronounced in all of the species, and is at once noted by the radial dot, and by the fact that its cells are filled with tannin. In the second particular, exception must be generally made of *O. Claytoniana.*

The stele is comparatively small, and is typically protostelic, since there is no pith. The wood has a narrow elliptical form, consisting mainly of very large scalariform tracheids. At each end of the ellipse there are a few small protoxylem elements, which are especially evident in the young root, and which have no connection with the protoxylem of the stem or leaf. The root, therefore, is diarch. There are likewise two bundles of phloem alternating radially with the bundles of xylem. In all of the Osmundas, however, I have observed triarch steles in the larger roots, which exception is of comparative frequence in *O. cinnamomea.* The phloem consists of two flat bundles or bands. These bands are made up chiefly of thin walled sieve tubes which are of the same kind as occur in the stem. None of them are "quergestreckt." The phloem is separated from the xylem by three or four rows of parenchyma, and from the endodermis by a two rowed parenchymatous pericycle.

DEVELOPMENT OF THE TISSUES FROM THE GROWING POINT.

In discussing this subject there are two points in particular which will receive special consideration: (1) the statements of Strasburger and Zenetti regarding the origin of the endodermis, and (2) the real nature of the "quergestreckte Zellen."

The determination of the relation of the tissues to the apical cells seems of little concern, and moreover in the study of the apical region of the growing point there are serious difficulties.

Having described these for *O. regalis*, Professor Bower aptly remarks :[25]

> The meristem being thus at times irregular, and the subdivisions of the segments being variable, it is to be expected that the study of it (the apical region of the growing point) in longitudinal section would present difficulties, and I have not been able to trace any definite and characteristic mode of segmentation. Longitudinal sections cut from a considerable number of stems show that a conical apical cell is present. The relations of the surrounding tissues, and their reference to regularly succeeding segments are difficult to recognize.

To these observations on the extreme apical end of the growing point we have nothing to add, but pass further down the stem.

A short distance from the apex of the stem, the various tissues, though in embryonic form, become apparent. The cylinder of wood, whose thin walled, unlignified cells are still provided with protoplasm and nucleus, can be distinguished from the pith, the parenchyma in the leaf gaps, and the immature phloem. The pericycle is rich in protoplasm, and its cells are radially arranged. At an earlier stage still, even before there is any evident differentiation in the vascular tissues, the leaf traces can be seen coming off from the cauline vascular axis.

When the protoxylem can be first demonstrated by phloroglucin and hydrochloric acid, the endodermis (both internal and external in the case of *O. cinnamomea*) is also demonstrable by the same reagents, though not before. Zenetti has claimed[26] that at the time the protoxylem is formed, the endodermis, pericycle, "quergestreckte Zellen," protophloem cells, and some cortical cells are all in the same radial rows ; and that, therefore, all have originated from the same mother layer. Strasburger has asserted[27] that the tissue lying in the stem between the phloem and the endodermis and occupying the position of a pericycle arises by tangential divisions with the endodermis out of the innermost cortical layer. Therefore, not the entire phloeoterma, he claims, but the outer division product is that which gives origin to the endodermis.

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[25] BOWER: The comparative examination of the meristems of ferns as a phylogenetic study. Ann. Bot. **3**: 323. 1889.

[26] ZENETTI: *op. cit.* 64.

[27] STRASBURGER: *op. cit.* 449.

Now, at the time the protoxylem elements appear, I did not find, in the species examined, the cells of the endodermis corradial with those lying centrad. It is true that in younger stages the cells in this region are in radial rows; but nearer still to the *punctum vegetationis* this is approximately true of all the cells of the stem. At this earliest stage one would hesitate to say, because certain cells were corradial, that they were therefore division products of the same mother cells; so Zenetti's conclusion, based on this sole argument, scarcely seems conclusive, even granting the correctness of his observation. If, too, such a conclusion were correct there would be the curious anomaly of certain phloem and cortical tissues having a common origin.

Evidently the study of transverse sections cannot settle the matter. To attempt to follow these layers upwards is obviously only possible in median longitudinal sections. But in the stems of the Osmundaceae the leaf traces are exceedingly numerous, and at the growing point are closely packed together, and appear before the tissues of the cauline central cylinder become at all differentiated. Hence, no matter what be the plane of section, the endodermis cannot be traced continuously very far anteriorly to the point at which it is differentiated, for a leaf trace is certain to intervene; and I found it quite out of the question to pick out an undifferentiated endodermis on the side of the leaf trace turned towards the apex. Therefore, every attempt failed to refer the endodermis and the rows of cells "occupying the place of the pericycle" to the same initial layer.

The typical protophloem, and the "quergestreckte Zellen" begin to be differentiated simultaneously with the appearance of the protoxylem. They are best examined in tangential sections. Their walls at this time become pitted, and their contents much less granular than those of the surrounding cells. Here, as in the maturer parts of the stem, there appear to be no differences between the typical protophloem and the "quergestreckte Zellen." Their relation to the leaf traces seems to explain their irregularity in orientation. Immediately below the point of origin of a leaf trace they are arranged with their long axes parallel to the long axis of the stem, and there is a gradual transition to the tangential position. More than this, the laterally placed protophloem cells of the leaf traces can be directly traced into the "quergestreckete Zellen" of the stem. There seems little doubt, therefore, as to their nature.

To summarize observations: (1) The "quergestreckte Zellen" are sieve tubes, as has been demonstrated above; (2) they become differentiated at the same time as the typical protophloem, and (3) occupy the same relative position; (4) they resemble the protophloem cells in form; (5) their orientation is not uniform; (6) they pass imperceptibly into the longitudinally orientated protophloem cells of the leaf traces. Hence there seems no reason to regard them as anything else than protophloem.

CONCLUSIONS.

The question now remains, how to interpret the vascular system of the Osmundaceae. To do this more intelligibly, it will be well to recapitulate the main fibrovascular theories. We shall begin with that of Sachs and DeBary.

These botanists regarded the bundle as the unit, and the vascular system as a more or less simple complex of bundles embedded in ground or fundamental tissue. Developmental studies have shown that this theory is inadequate, for the unit is wrong.

The hypothesis which at present obtains was supplied by Van Tieghem and Strasburger. In this conception[28, 29, 30] the stele is the unit. The primitive form of stele, the monostele, such as occurs for example in most roots and in the stems of lycopods, is a solid central strand of xylem, surrounded by a sheath of phloem, and marked off from the cortex by the differentiated internal cortical layer, the endodermis. Of this there are many modifications, of which mention is made of the most important. By the repeated bifurcation of the monostele, the polystelic type is

[28] VAN TIEGHEM: Traité de Botanique 673, 765.

[29] VAN TIEGHEM: Sur la polystélie. Ann. Sci. Nat. Bot. VII. 3: 275.

[30] VAN TIEGHEM: Éléments de Botanique 1: 84, 179.

presented, as in Primula and Pteris, each segment being in every respect a stele. If these steles fuse laterally, thus forming a ring with internal and external phloem, the gamostele is produced as illustrated by Marsilia. Again, when parenchyma segregates in the axis of the monostele, and the vascular ring is broken into strands by ectad extensions of this pith (the medullary rays), we have the medullated monostelic type, such as is common in phanerogams. It is to be noted that the medullary and cortical tissues are considered by both these botanists to be of morphologically different value. Now by the bending in of the endodermis of the medullated monostele between the bundles, and the fusion of the ends of adjacent groups on the centrad side of the bundle, so that each bundle has its endodermal sheath, and medulla and cortex become continuous, the schizostelic or astelic type results. Of this phenomenon Ranunculus and Equisetum afford examples. A modification of this type, the gamódesmic-schizostelic, is produced by the lateral fusion of these endodermal sheaths, so that there is a common internal and a common external endodermis. If the internal endodermis degenerates, as it does in *E. arvense*, then there is evidently a simulation of the medullated monostele. It is fair to add that Strasburger dissents[31] from the last two types described, the astelic and the gamodesmic, for he regards the endodermal sheaths about the bundles in the first of these, and the internal endodermis in the second, as not morphologically phloeotermal, but originating from specialized stelar cells.

The researches of Gwynne-Vaughan[32] and Jeffrey[33] have shown that the phenomena said to lead up to polystely do not occur in Primula and Pteris. If the polystelic conception falls, obviously gamostely goes too. Further, astely has been shown, where it occurs in Equisetum and Ranunculus, to be preceded by the gamodesmic appearance. Later the internal and external

[31] STRASBURGER: *op. cit.* p. 442.

[32] GWYNNE-VAUGHAN: Polystely and the genus Primula. Ann. Bot. **11**: 307. 1897.

[33] JEFFREY: Morphology of the central cylinder of angiosperms. Trans. Canad. Inst. **6**: —. (1–40) 1900.

endodermis may fuse between the bundles, but in no case is there an inward looping of the endodermis. Finally, the stelar origin of the pith of the medullated monostele has been disputed, and the question raised as to whether the medullary and cortical tissues are in reality morphologically different. In other words, is the medullated monostelic type primitive, as its simplicity might indicate, or has it resulted by degeneration from more complex types?

It is interesting to note that Potonié had discussed this last question from the standpoint of fossil botany, and concludes[34] that it seems evident in the case of certain groups, such as the cycads, that the simple results from the complex (for example, the cycads from the Medulloseae). Hence for these groups at least he is inclined to reject this idea of segregation of parenchyma in the center of the protostele to form the medullated monostele, but holds that the medullated monostelic type has probably arisen by degeneration from his "pericaulom." Since this pericaulom was produced, according to his theory, by the lateral fusion of leaf bases in the stem surrounding the originally solid stele, the "urcaulom," the medullated monostele has been derived from a form of central cylinder such as Van Tieghem has described as polystelic, preceded or accompanied by the disappearance of the enclosed urcaulom. The paleontological evidence, however, appears not to be conclusive, for in the very group that Potonié cites, the cycads, so eminent a paleobotanist as Dr. D. H. Scott takes a directly opposite view. He points out[35] that the vascular system of the Medulloseae was typically polystelic, while in the recent cycads there is but one vascular cylinder, and that hence "we should involve ourselves in unnecessary complications if we endeavored to derive the simple, primary structure of the cycadean stem from the more elaborate organization of a Medullosa. It is far more natural to suppose that the monostelic cycads arose from monostelic ancestors."

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[34] POTONIÉ: Die Metamorphose der Pflanzen im Lichte palæontologischer Thatsachen 22.

[35] SCOTT: Studies in fossil botany 395. 1900.

In 1897, Dr. E. C. Jeffrey put forward another view of the vascular system,[36] based upon a study of the young sporophyte. Here, too, the stele is the unit. According to this conception there are two primitive types of vascular axes; the first the same as Van Tieghem's primitive type, and designated "protostelic;" the second, one in which there is a hollow cylinder, or "siphonostele," whose external wall abuts on the cortex, and whose internal wall encloses the medulla, and which possesses internal as well as external phloem. This is the "amphiphloic siphonostelic" type, called by Van Tieghem the "polystelic." The commonly called "astelic" modification results from the amphiphloic type by a degeneration of the internal phloem, and the medullated monostelic type of Van Tieghem is derived from the astelic by the loss of the internal phloeoterma or endodermis. A study of development from the seedling is likely to show how these and other modifications in the stellar structure have been derived from the primitive types. Attention is also called to certain portions of the wall of the siphonostele in which the vascular tissues do not develop. These places lie above the points of exit of branch traces, and of leaf traces, and are known as ramular and foliar gaps respectively. Through these gaps the tissues outside and inside connect. In transverse section, the connecting tissues seen constitute the medullary rays, and the segments of the woody cylinder with adjacent phloem and parenchyma the bundles. A fact of great phylogenetic importance in dealing with "gaps" was further pointed out, namely, that in small leaved plants, as in the Lycopodiaceae, Equisetaceae, etc., only ramular gaps occur. These plants are grouped in the division Lycopsida, and their steles are said to be cladosiphonic. In all other vascular plants there is a gap for every leaf. These constitute the large leaved plants, the Pteropsida, and their steles are said to be phyllosiphonic.

As a matter of theory, it is suggested that the siphonostele arose from the protostele for mechanical causes, in the Lycopsida to support the branches, and in the Pteropsida to support the

[36] JEFFREY: Trans. Brit. Assn. Toronto. 1897.

leaves. Potonié also explains the origin of his second primitive type the "pericaulom," the homologue of the siphonostele, on mechanical grounds.

In the light of these theories we can now apply ourselves to an interpretation of the anatomy of the vascular system of the Osmundaceae, and likewise note if the facts already dealt with throw any light on the theories.

First, we are in a better position now to decide whether the internal endodermis of *O. cinnamomea* is phloeotermal or not. It has been noted that in similar cases, that is, in gamodesmic stems, Strasburger has denied the phloeotermal character of the internal endodermis. With regard to the internal endodermis the following facts have been observed:

1. There is present the characteristic cuticularized "radial dot."

2. The structure and contents of the cells are materially the same as of the external endodermis.

3. The sheath is continued into the portions which in some individuals present the phenomenon of internal phloem, just as in any form called by Van Tieghem and Strasburger gamostelic. In the gamostelic type the phloeotermal character of the internal endodermis has been admitted.

4. It generally connects with the external endodermis through ramular gaps, and by no means rarely through foliar gaps. When this occurs, there is no point at which it could be said that the one stops or the other begins.

Having verified these facts in a great many cases, I am therefore of the opinion that the internal and the external endodermis are homologous tissues.

Second, are the medullary tissues morphologically equivalent to the cortical? Again we recapitulate observations.

1. They do not differ in structure or in contents.

2. The medulla very often contains brown sclerenchyma, at least in three species studied, a tissue which, in other ferns, never constitutes a part of the stele.

3. Medulla and cortex connect more frequently than not

through the ramular gaps in *O. cinnamomea*, and occasionally through foliar gaps; and neither is there a transition in the nature of the connecting tissues, nor any line at which we can say, the cortical tissues lie externally to this and the medullary tissues internally.

4. The cortical and the medullary brown sclerenchyma sometimes fuse through ramular gaps in *O. cinnamomea*.

5. Portions of stem of *O. cinnamomea* have been found which are of the "gamostelic" type of Van Tieghem. The medulla in gamosteles is granted to be morphologically a cortical tissue.

The conclusion is evident for *O. cinnamomea* at least, and if it be granted that the medullary tissues of this species are morphologically equivalent to the cortical tissues, then biological principles alone would demand a like conclusion for the other species.

Third, of what type is the vascular system of *O. cinnamomea?* Again the facts must form the basis for a decision:

1. The young stem of *O. cinnamomea* possesses an entirely closed hollow vascular cylinder, sheathed with phloem and broken only immediately above the exit of a leaf trace; and at a level higher up the cylinder is entirely closed again. There is a medulla and an internal endodermis.

2. In older plants the leaves are more frequent, and the gaps extend through several internodes; but yet the cylinder is the unit. The cylinder of phloem is quite rarely broken, except where branching takes place.

3. There is an internal endodermis which is persistent throughout the entire central cylinder of the stem.

4. As a rule the internal endodermis bends out opposite leaf gaps.

5. There is an internal phloem in portions of some plants.

6. Not only does the cylinder of external phloem remain practically unbroken, but opposite leaf gaps there is on the inner side a proliferation of sieve tubes. In *O. regalis* Janczewski found isolated sieve tubes in the parenchyma filling the leaf gap; and the same thing is true of *O. cinnamomea*.

According to Van Tieghem's stelar theory, the last two facts can be explained only by considering the central cylinder of the Osmundaceae to be "gamostelic." The centrad extensions of the phloem opposite the medullary rays could then be explained by assuming that steles had united laterally, with the disappearance of phloem on the medullary side, but with the partial persistence of phloem on the radial planes. This would also explain the occurrence of internal phloem, the union of internal and external endodermis, and the homology of medullary and cortical tissue. But from the study of development there is not a shred of evidence to prove that there has been a union of steles. In fact, such a study shows distinctly that there is but one stele in the stem of *O. cinnamomea* from the very first. Van Tieghem's observations on *O. regalis* have already been quoted (see INTRODUCTION); so we cannot describe the cauline vascular system as "gamostelic," if this name implies a union of steles.

There remains yet another interpretation, namely, that the vascular system of the stem of *O. cinnamomea* is a siphonostele in which some degeneration from the primitive type has taken place. It has been pointed out in a description of the conception of the vascular system held by Dr. E. C. Jeffrey that the most primitive siphonostele is the amphiphloic siphonostele. In this there is an internal phloem and phloeoterma, and in its phyllosiphonic form there are wide leaf gaps and branch gaps through which internal and external phloem, internal and external phloeterma, and medulla and cortex connect with each other. In *O. cinnamomea* the gaps in this primitive type have closed somewhat, so that medulla and cortex rarely connect except through ramular gaps. Also the phloem forms an almost unbroken cylinder, and the centrad proliferations opposite the medullary rays are the vestigial relics of connection between external and internal phloem. The internal phloem has also disappeared in greater part.

With such a conception of the cauline vascular system of *O. cinnamomea*, the centrad accumulation of sieve tubes opposite the medullary rays, the occasional presence of sieve tubes in the medullary rays, the fact of the internal phloem, the connection of medulla and cortex through ramular and foliar gaps, the presence of sclerenchyma in the medulla, the bending out of the internal endodermis into the leaf gaps, and the facts of development, all become intelligible.

Fourth, which of the species studied possesses the most primitive type of central cylinder?

After a fairly comprehensive study there is one feature that stands out prominently, the great similarity and uniformity of vascular structure in the various species of Osmunda and Todea. According to Solms-Laubach the stems of fossil remains of this family, of which none earlier than the Tertiary have been found, do not present any striking differences from the living representatives. Paleobotany, therefore, offers no solution to the problem. In spite of the conservatism of the central cylinder, there are, however, minor anatomical differences. On the basis of these alone, without referring to the young sporophytes, I think there is sufficient warrant for placing *O. cinnamomea* at one end of the series, possessing as it does an internal endodermis, internal phloem, and wide ramular gaps. It is difficult to say which species is to be placed at the other end of the series. In view of the fact that *O. Claytoniana* never has sclerenchyma in the medulla, that there are small or even no ramular gaps, no internal sclerenchyma, and even a degenerated external endodermis, we may not be far astray in putting it in the position farthest from *O. cinnamomea.*. Now of these two, which retains a central cylinder more nearly primitive? If *O. regalis* has a medullated monostelic central cylinder, as has hitherto been claimed for it, then *O. Claytoniana* has also, and therefore, according to Van Tieghem, a more primitive form than that of *O. cinnamomea.* Assuming the correctness of this for the moment, it will be in order next to see if such phenomena as presented by *O. cinnamomea* could be derived according to Van Tieghem's hypothesis from such a simple medullated monostelic form as that of *O. Claytoniana.*

The phloem sheath must have broken into bundles, and the endodermis must have looped in between the bundles, and connected around them on the centrad side. With the formation of this astelic type some of the cortex would have been included in the medulla, in evidence of which the sclerenchyma in the pith would stand as proof. Then next the bundles must have fused laterally to produce the gamodesmic type in which there is an external and an internal endodermis. Granting that the central cylinder could be so plastic in a single species, there are left yet to be explained the continuous sheath of phloem, the proliferation of sieve tubes opposite the medullary rays, the occurrence of isolated tubes in the medullary rays, the occurrence of internal phloem, and the phenomena of the ramular gaps. Further, there are no facts in development that point to such a series of changes.

Turning now to the other alternative, namely, the possibility that *O. cinnamomea* has the more primitive form of central cylinder, it will be granted that by the degeneration of internal phloem, endodermis, and medullary sclerenchyma, and by the closing of the ramular gaps the central cylinder such as we find in *O. Claytoniana* would result. In proof that such degeneration could have taken place, it is to be noted (1) that in *O. cinnamomea* itself, it has been pointed out that the amphiphloic condition is localized, that the internal endodermis has already begun to degenerate, that medullary sclerenchyma is not a constant feature, and that closed steles above the point of branching are not at all uncommon; and (2) in further proof, analogous cases of degeneration within the same genus are frequent. Thus within the genus Equisetum two species such as *E. arvense* and *E. hiemale* may be chosen, the first long considered medullated monostelic and more primitive, the second gamodesmic and considerably modified. But a study of development and of nodal portions of the stem has shown that *E. arvense* has a reduced central cylinder, the product of degeneration from a gamodesmic type, and that therefore *E. hiemale* is nearer the primitive. Similar cases of degeneration have been pointed out by Van

Tieghem, Poirault, and Jeffrey, in the genera Ophioglossum, Botrychium, Equisetum, Ranunculus, etc. Very lately Boodle,[37,38] has called attention to an interesting series of central cylinders in the family Schizaeaceae. *Aneimia Phyllitidis* has a ring of separate bundles, each with a band of xylem surrounded by a phloem, pericycle, and endodermis of its own; *A. Mexicana* has a complete ring of xylem in the internodes with external and internal cylinders of phloem and endodermis; Schizaea has a ring of xylem surrounding a central pith, but no internal phloem or endodermis. It is likely that here, too, the Schizaea type is derived from the Aneimia type by degeneration. In the Hymenophyllaceae likewise, every grade is found from the case in which the phloem of the solid stele forms a complete ring to that in which it is developed on one side only.

After examining a number of comparatively young specimens of *O. Claytoniana*, I am somewhat doubtful if the study of the development of this species will throw any further light on the subject of morphology; but for *O. regalis* I am more hopeful. Nevertheless, aside from further developmental proofs, I incline to the view that *O. cinnamomea* possesses the most primitive type of central cylinder. I again recapitulate the reasons:

1. The opposite view demands a very plastic central cylinder in one species alone, not differing very greatly in habit from the others.

2. There would still remain phenomena that the opposite view could not explain.

3. There are no facts of development even in analogous cases to support the opposite opinion.

4. The view adopted here demands only slight changes, and those are of degeneration, to explain all the phenomena.

5. There are precisely similar analogous cases of degeneration.

6. Within the species *O. cinnamomea* itself, every phase of

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[37] BOODLE: Stem structure in Schizaeaceae, etc. Brit. Assn. Dover, 1899.

[38] BOODLE: On the anatomy of the Hymenophyllaceae. Ann. Bot. 14: 455. 1900.

degeneration except the entire disappearance of internal endodermis is observable in suitable specimens.

When we attempt to orient the other species amongst themselves, the task is more difficult, and of little importance. As already indicated, a closer study of development may afford more precise proofs. In the mature stems we have seen that *O. regalis* occasionally has sclerenchyma in the medulla, that there are ramular gaps, though usually small, and that the external endodermis is well developed. In *O. Claytoniana*, on the other hand, sclerenchyma is never found in the medulla, ramular gaps are infrequent, and the external endodermis shows indications of degeneration. In neither of these species is internal endodermis or internal phloem present. The probability, therefore, is that in the genus Osmunda there is a series, *O. cinnamomea* possessing the most primitive type of central cylinder and *O. Claytoniana* the most degenerate, *O. regalis* occupying a middle position, but nearer to the latter. It is merely interesting to note in passing that Professor Campbell concluded[39] from his study of the prothallia of *O. Claytoniana* and *O. cinnamomea*, that the gametophyte of the former was more specialized in many particulars, in other words, was less primitive in type than the latter.

Fifth, does a study of the vascular system help to determine the phylogenetic position of the Osmundaceae?

It was stated at the beginning of this paper that botanists have regarded the Osmundaceae as possessing an anomalous form of central cylinder among the Filicales, their reason being that it seemed to present more of the features of a central cylinder such as is typical for dicotyledons, that is, a medullated monostele in Van Tieghem's terminology. In determining the position of the family, therefore, in any natural system of classification, it was hopeless to try to reconcile this single dicotyledonous character with the remaining filicinean characters, and so the vascular system in the family was regarded as anomalous.

[39] CAMPBELL: On the prothallium and embryo of *O. Claytoniana* and *O. cinnamomea*. Ann. Bot. **6**: 49. 1892.

It is fair to note that Zenetti dissented[40] from the prevailing view, and evidently for the reason that he attached some value to the nature of the central cylinder from the phylogenetic standpoint. Hence he sought to find the same type amongst the vascular cryptogams. He rejected the ordinary fern type because it is "polystelic," and the lycopod type because there is no pith, obviously overlooking *Selaginella laevigata*, Phylloglossum, etc. So finding no living form with which comparison could be established he turned to paleophytology. Among the Lepidodendraceae he found the prototype sought for, especially in such of these fossils as *L. Harcourtii*, and the Sigillarians, because in these the wood is broken into bundles between which there are medullary rays. But he evidently did not grasp the significance of bundles and medullary rays in relation to leaf traces and branch traces. In *O. regalis*, too, the protoxylem is endarch, while in those ancient lycopods it was exarch. The stele of the Lepidodendraceae, as in all plants bearing palingenetically small leaves, was cladosiphonic, while *O. regalis* is phyllosiphonic, as are all primitively megaphyllous plants. Hence any attempt to establish a relation between the central cylinder of modern ferns and of those ancient horsetails must fail. Indeed, of the early fossil forms preserved, the one with a central cylinder most closely resembling that of the Osmundaceae, as has been pointed out by Dr. Scott,[41] seems to be the cycadofilicinean Lyginodendron (*fig. 26*).

Further, we dissent just as strongly from the view that the family is anomalous in the matter of its vascular system. The typical fern stem possesses an amphiphloic siphonostele, as is especially revealed by a study of development. But degenerated forms of this are to be met with in almost every family, some examples of which have been noted. The Osmundaceae, as has been shown above, all exhibit some degree of degeneration from this type. It is therefore evident that the cauline vascular system of this family is neither primitive nor anomalous among the Filicales.

[40] ZENETTI: *op. cit.* 73.

[41] SCOTT: *op. cit.*

SUMMARY OF OBSERVATIONS.

1. An internal endodermis has been demonstrated in *Osmunda cinnamomea*, but in none of the other species examined. This internal endodermis is in textural continuity with the external endodermis through branch gaps, and sometimes through foliar gaps.

2. Internal phloem has been found in *O. cinnamomea* in the region of branching. This is continuous with the external phloem through ramular gaps.

3. The external phloem of the Osmundaceae forms a continuous cylinder, a fact which De Bary has stated for *O. regalis;* and is not broken opposite the medullary rays as Strasburger has affirmed of the same species. Isolated sieve-tubes have been found in the medullary rays of *O. cinnamomea.*

4. The xylem forms a cylinder broken only by foliar and ramular gaps.

5. Brown sclerenchyma has been shown to be usually present in the medulla of *O. cinnamomea*, not uncommonly in *O. regalis*, and not at all in *O. Claytoniana.* It occurs likewise in *Todea barbara*, but has not been observed in *T. superba.*

6. The medullary and cortical tissues of the Osmundaceae are histologically equivalent. Brown sclerenchyma, which is not an intrastelar tissue in other ferns, occurs in both medulla and cortex; and in *O. cinnamomea* the brown sclerenchyma of the medulla is in continuity with that of the cortex.

7. In *O. cinnamomea* the typical ramular gap is one through which internal and external endodermis, internal and external phloem, cortex, and medulla connect. Every stage of degeneration has been observed in *O. cinnamomea*, however, down to the completely closed steles. *O. regalis* has a gap in the wood only, and *O. Claytoniana* usually none.

8. The so-called "quergestreckte Zellen" pointed out by DeBary in *O. regalis*, and more fully described by Zenetti, have been found in all the species studied. They are sieve tubes, possessing all the characteristic features of sieve tubes, even that of callus plugs. Their irregularity of orientation is shared by the other peripheral tissues of the central cylinder, and is

apparently due to disturbance caused by the exit of the large leaf traces.

9. Callus plugs have been demonstrated in the sieve tubes.

10. A study of the growing point has further shown that the "quergestreckte Zellen" and the typical protophloem are of the same kind; but it has failed to verify Strasburger's statement that the pericycle and the endodermis arise from a common maternal layer.

11. The phloem forms a continuous sheath in the leaf.

12. The root possesses a protostelic, diarch, occasionally triarch, vascular axis.

SUMMARY OF CONCLUSIONS.

1. The internal endodermis in *O. cinnamomea* is to be regarded as phloeotermal in nature, a fact denied by Strasburger in homologous cases.

2. The medullary and cortical tissues seem to be morphologically equivalent.

3. Observations on the anatomy of the Osmundaceae have been confined heretofore to the cosmopolitan *O. regalis*, and the subtropical Todeas. From these observations it was concluded by Van Tieghem that this family possessed a type of central cylinder anomalous among the vascular cryptogams, a type (the medullated monostelic type) peculiar to the phanerogams. The writer dissents from this view. It appears to be the case that the central cylinder of *O. cinnamomea* is not medullated monostelic, for the medulla is obviously extrastelar. Further, it cannot be regarded as gamodesmic on account of the topographical distribution of the phloem. The most obvious interpretation seems to be that it is a degenerate form of the amphiphloic siphonostelic type of central cylinder (polystelic type of Van Tieghem). *O. cinnamomea*, *O. regalis*, *O. Claytoniana* form a series arranged in order of degeneration of their central cylinders, and the same is true of *T. barbara* and *T. superba*.

The present research was carried on in the Biological Department of Toronto University under the direction of Dr. E. C.

Jeffrey, to whom I wish here to express my obligations for his advice throughout. My thanks are due to Professor R. Ramsay Wright for the facilities afforded in the department. For some of the material used I am indebted to Mr. Oakes Ames, Assistant Director of the Botanical Gardens, Harvard University; Sir William Thistleton Dyer, Director of the Royal Gardens, Kew; Dr. Brodie, Toronto; and Mr. R. B. Thomson, B. A.

University of Toronto.

EXPLANATION OF PLATES XIV–XVII.

Abbreviations used.

cp, callus plugs.
c, cortex.
e. c., external cortex.
i. c., internal cortex.
e, endodermis.
e. e., external endodermis.
i. e., internal endodermis.
lt, leaf trace.
m, medulla.
m. r., medullary ray.
p, pericycle.
ph, phloem.
p. ph., protophloem.
px, protoxylem.
qu, "quergestreckte Zellen."
r, root.
s. s. s., strands.
sc, sclerenchyma.
x, xylem.

PLATE XIV.

Fig. 1. Transverse section of the stem of *Osmunda cinnamomea.*

Fig. 2. Transverse section of part of central cylinder of *O. cinnamomea.*

Fig. 3. Tangential section of *O. regalis.*

Fig. 4. "Quergestreckte Zelle" of *T. barbara*, showing sieve plates and callus plugs.

Fig. 5. Transverse section of leaf trace of *O. Claytoniana* near the growing point.

Fig. 6. Transverse section of part of central cylinder of *O. cinnamomea.*

Fig. 7. Sieve tubes of *T. barbara*, showing sieve plates, "globules brilants," and callus plugs.

Fig. 8. Transverse section of part of central cylinder of *O. Claytoniana.*

PLATE XV.

Fig. 9. Tangential section of *Todea barbara*, showing "quergestreckte Zellen."

Fig. 10. Transverse section of *O. cinnamomea*, immediately above point of ramification, showing open branch gaps.

FIG. 11. Transverse section of *O. cinnamomea* through nearly the same region in another plant.

FIG. 12. Transverse section of same plant as in *fig. 11*, but lower down.

FIG. 13. Transverse section of same plant as in *fig. 12*, but lower down.

FIG. 14. Transverse section of the central cylinder of *O. cinnamomea*, showing internal endodermis and brown sclerenchyma in the medulla.

PLATE XVI.

FIG. 15. Transverse section of central cylinder of *O. cinnamomea*, showing internal endodermis and an absence of brown sclerenchyma in the medulla.

FIG. 16. Transverse section of the stem of *O. cinnamomea* in the region of forking, showing absence of ramular gaps.

FIG. 17. Transverse section of the stem of *O. Claytoniana*.

FIG. 18. Transverse section of the stem of *O. Claytoniana* in the region of forking.

FIG. 19. Transverse section of the stem of *O. regalis* in the region of forking.

FIG. 20. Transverse section of the central cylinder of *O. regalis*, showing brown sclerenchyma in the medulla.

PLATE XVII.

FIG. 21. Transverse section of the central cylinder of *O. cinnamomea*, showing internal phloem.

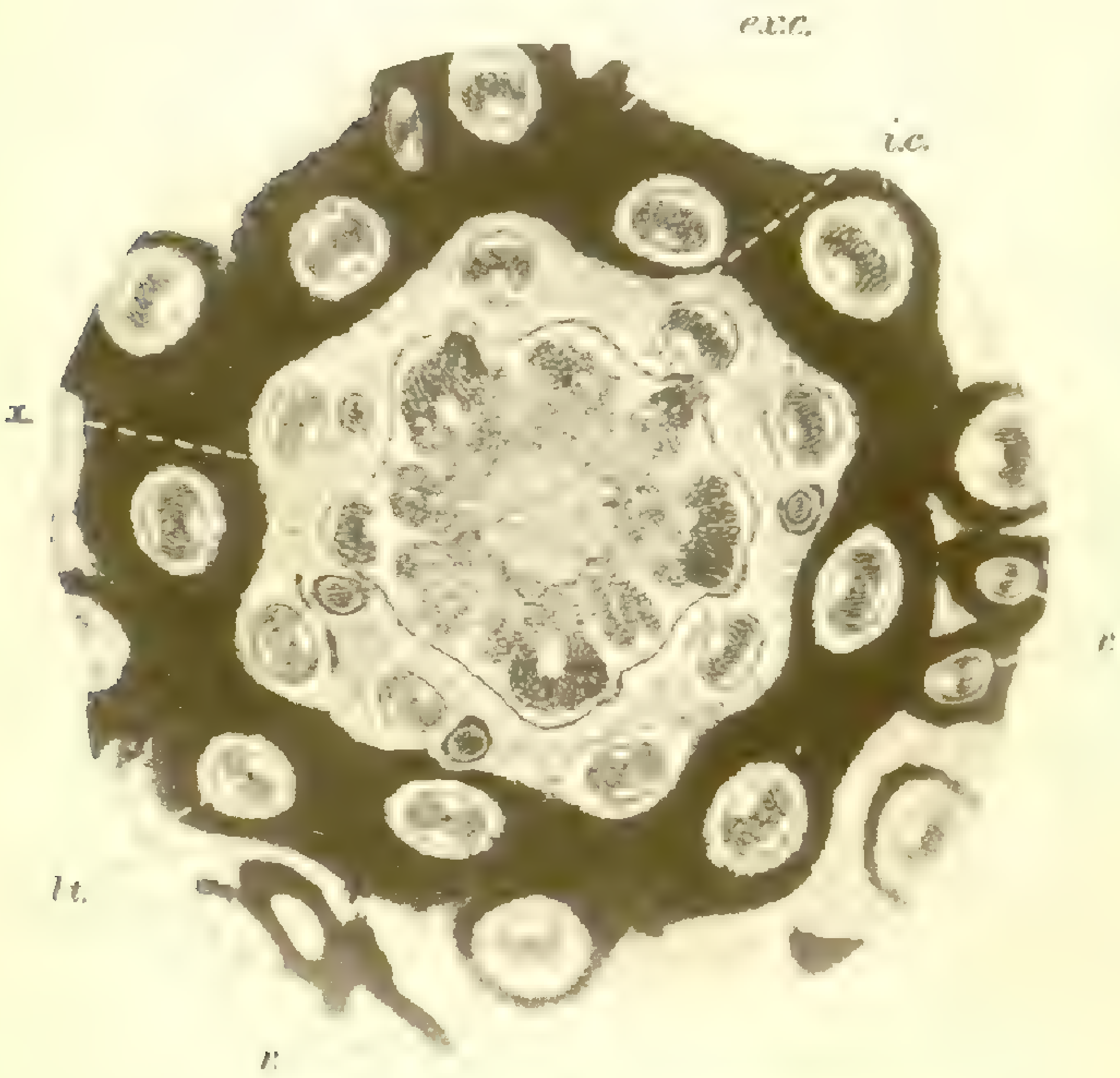
FIG. 22. A part of the central cylinder of *O. cinnamomea* shown in *fig. 21* more highly magnified.

FIG. 23. A transverse section of the young sporophyte of *O. Claytoniana*, showing one foliar gap, und the corresponding leaf trace opposite.

FIG. 24. Transverse section of the stem of *T. barbara*, showing brown sclerenchyma in the medulla.

FIG. 25. Transverse section of a part of the stem of *T. barbara* nearer the growing point.

FIG. 26. Transverse section of *Lyginodendron Oldhamium*, showing a leaf gap, a leaf trace opposite, strands of sclerenchyma in the medulla, and strands of primary xylem centrad of the cylinder of secondary xylem.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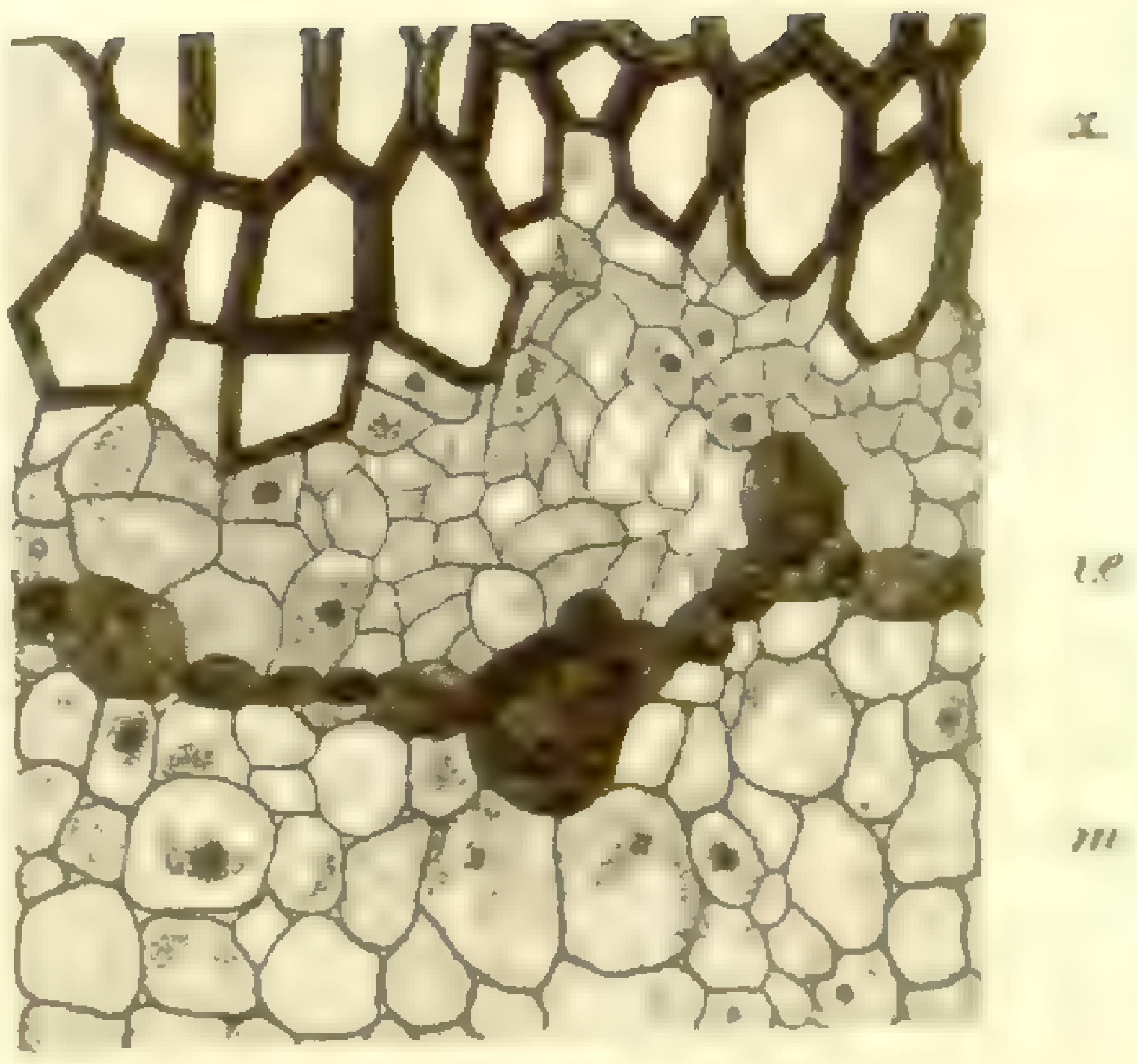

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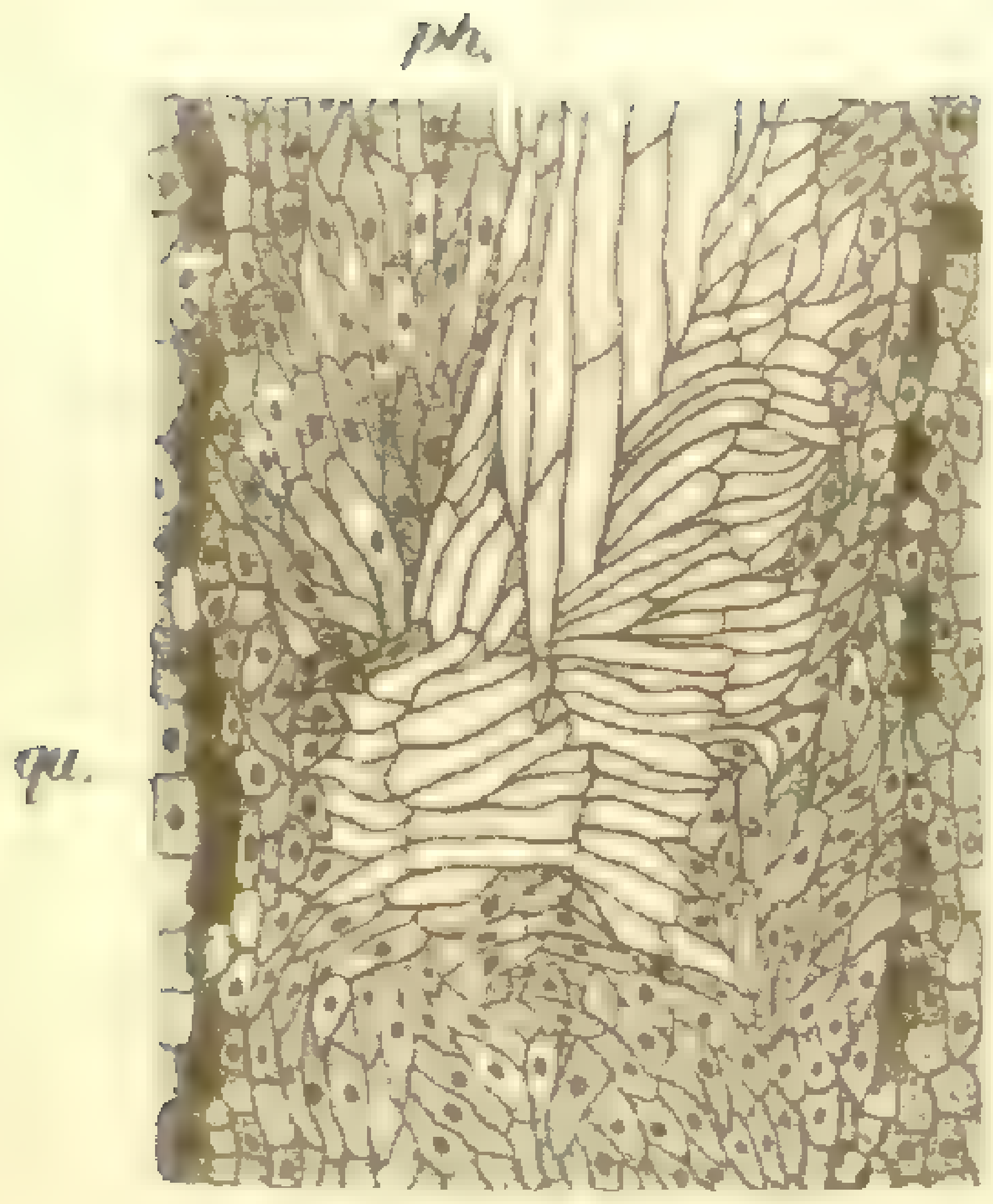

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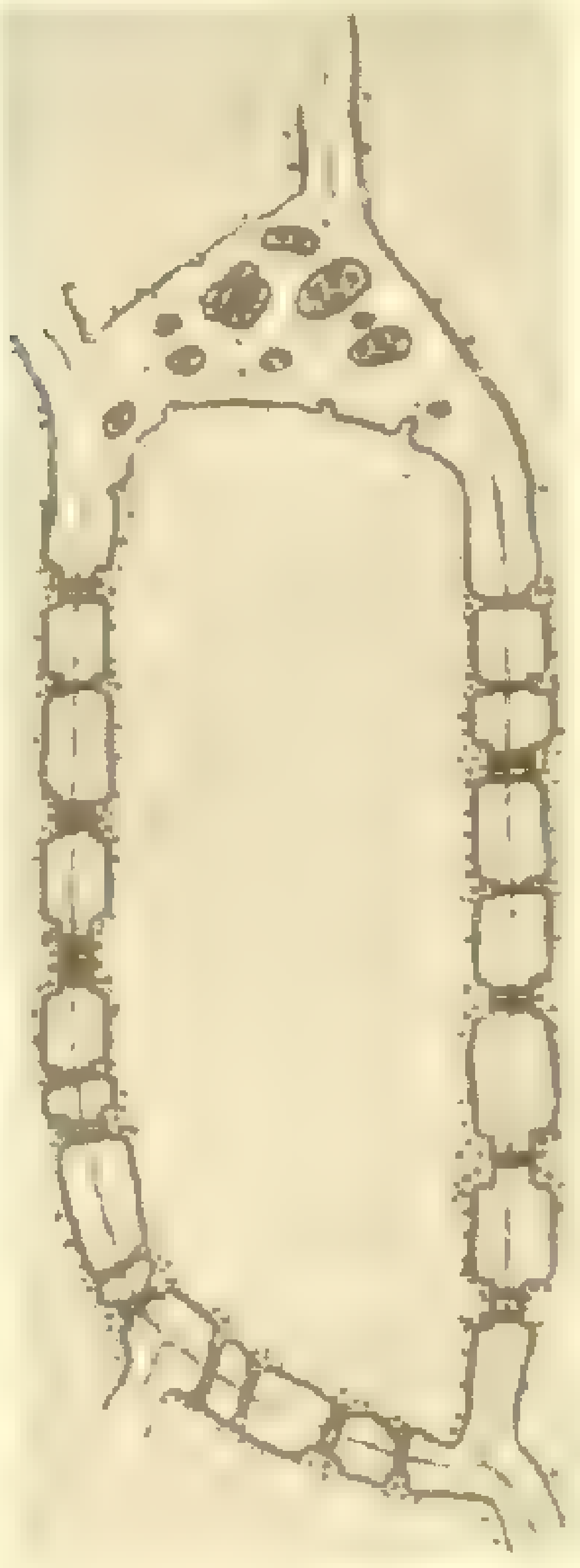

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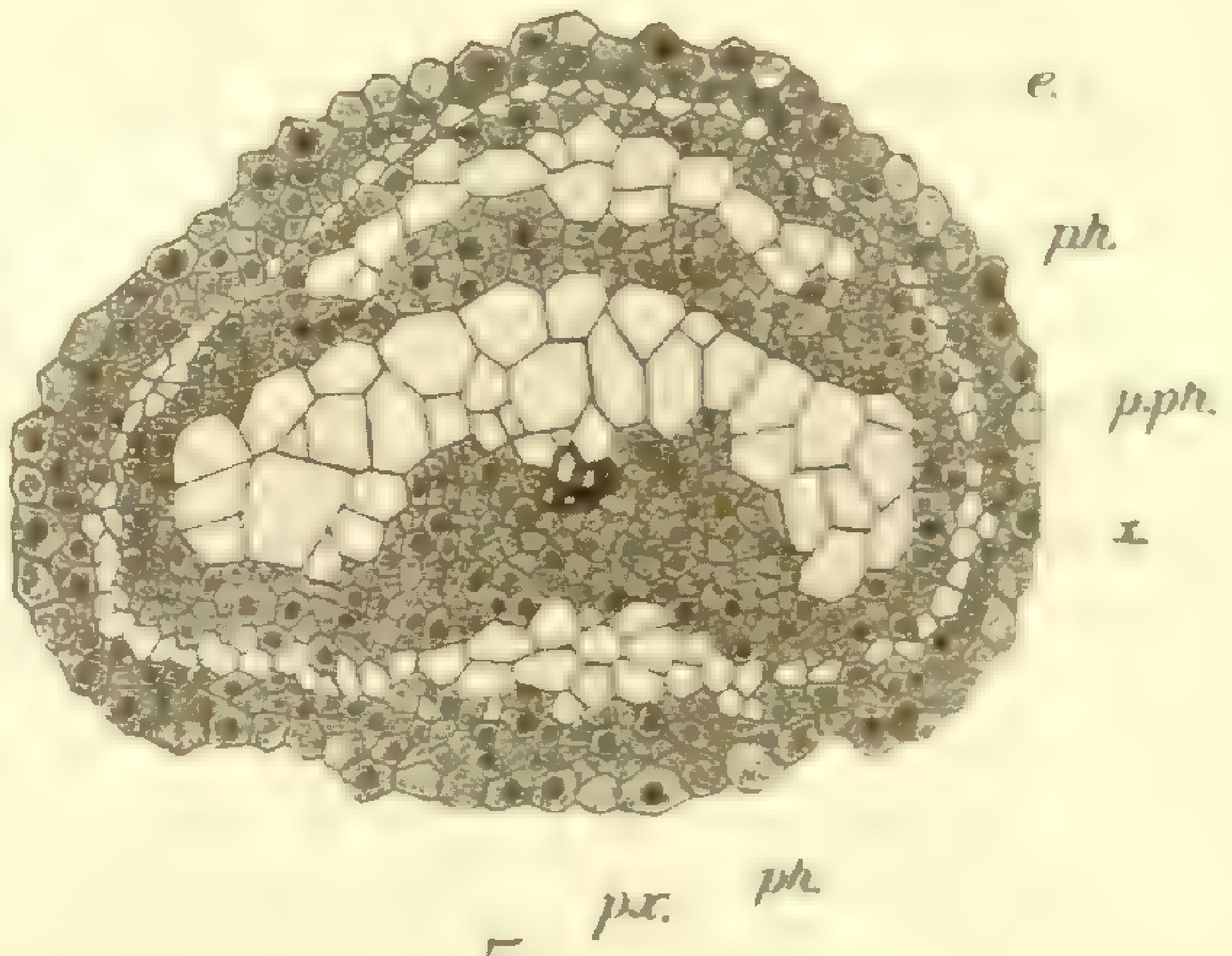
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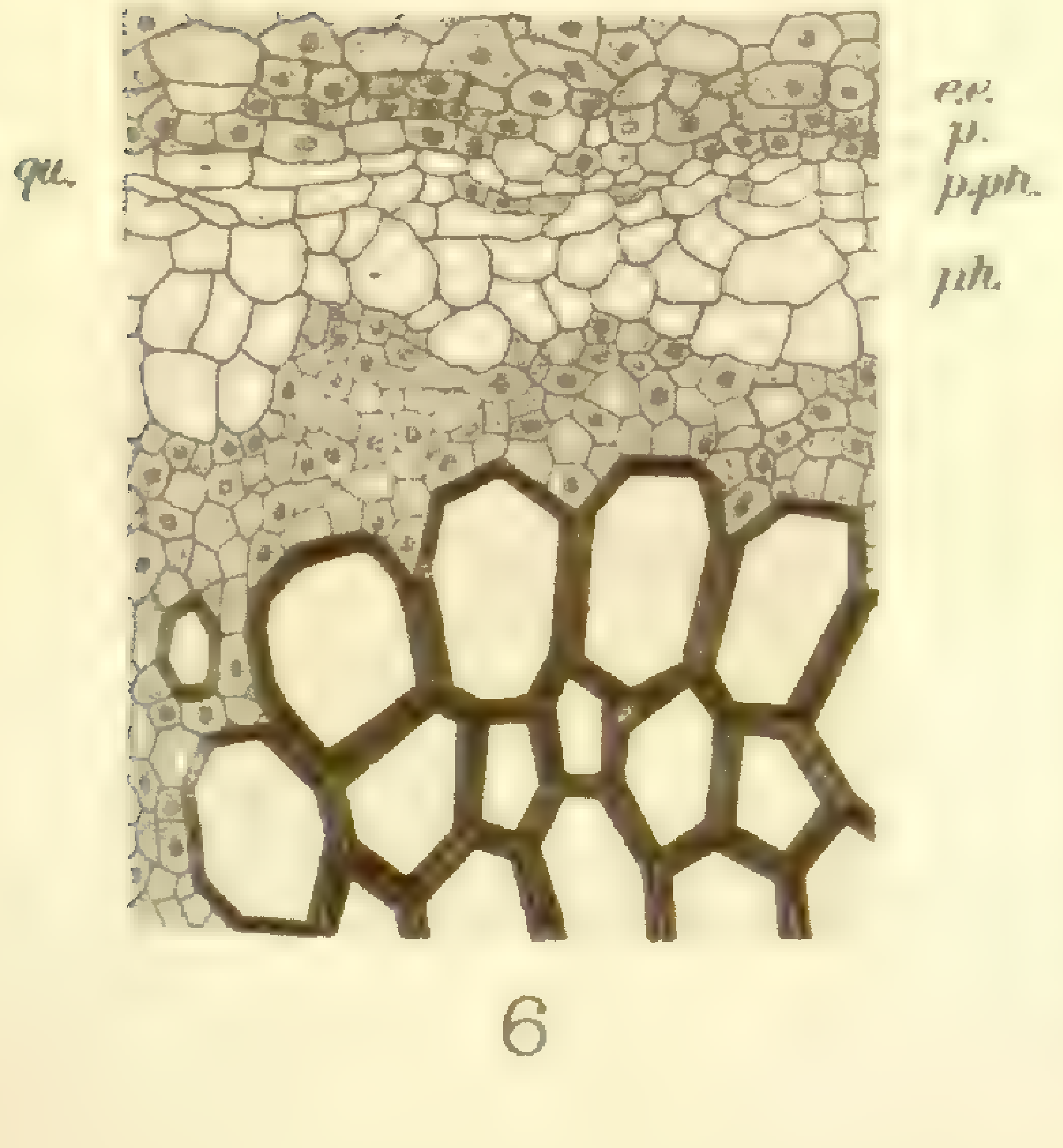
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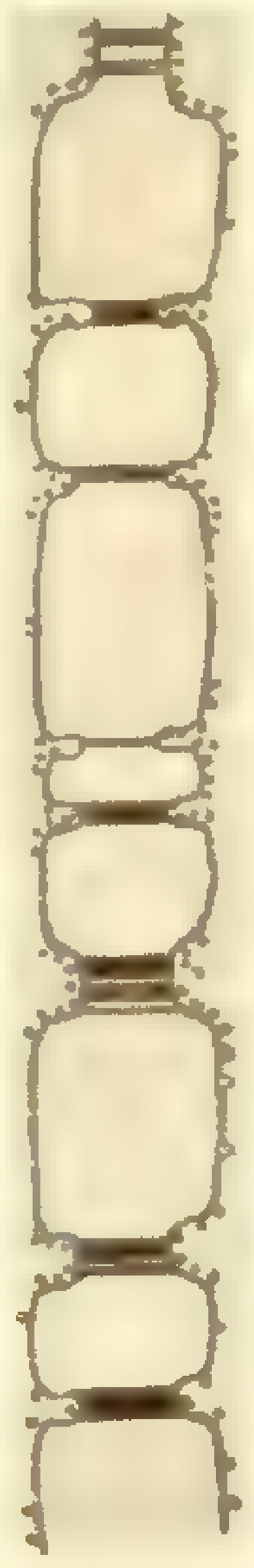

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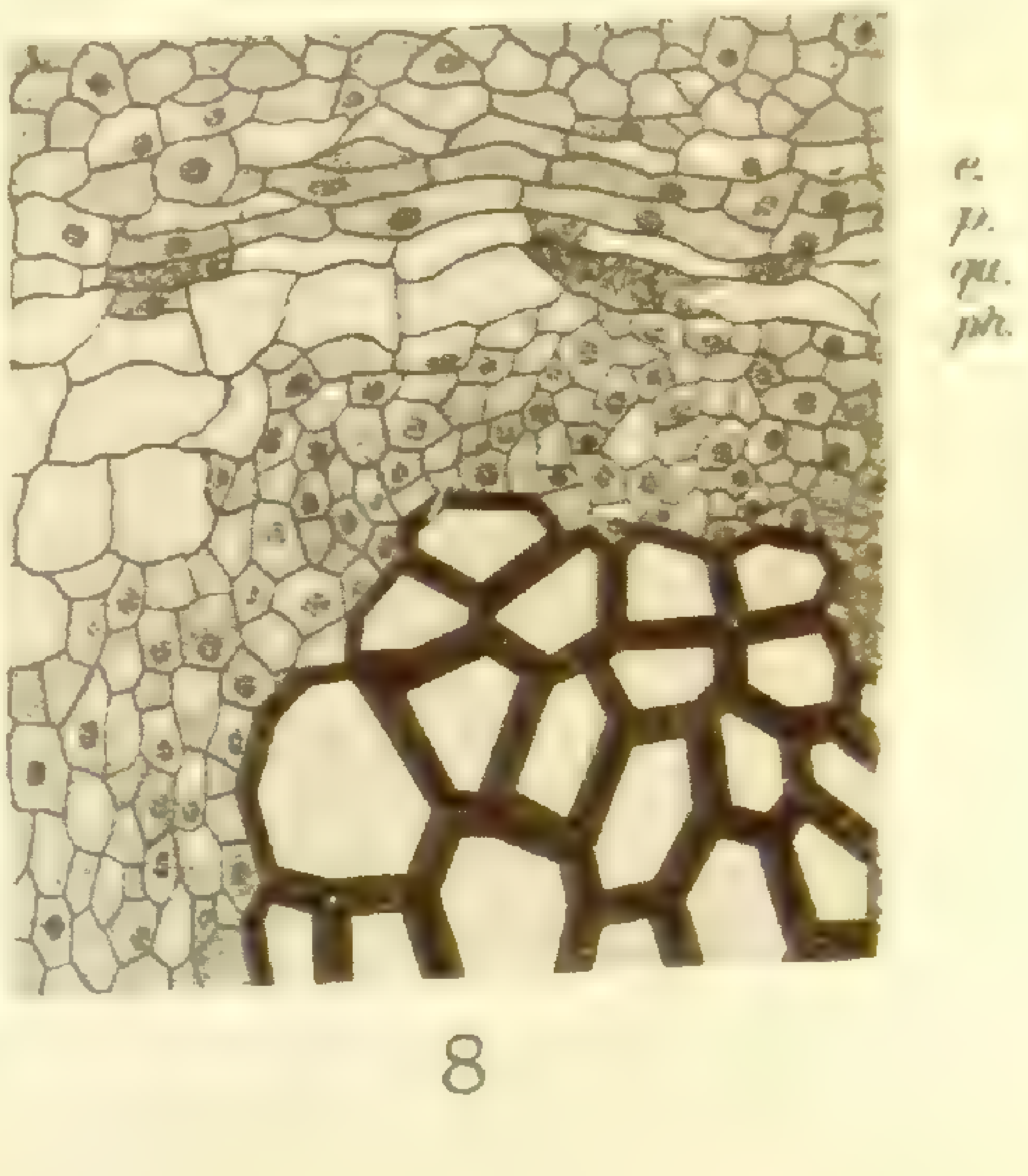

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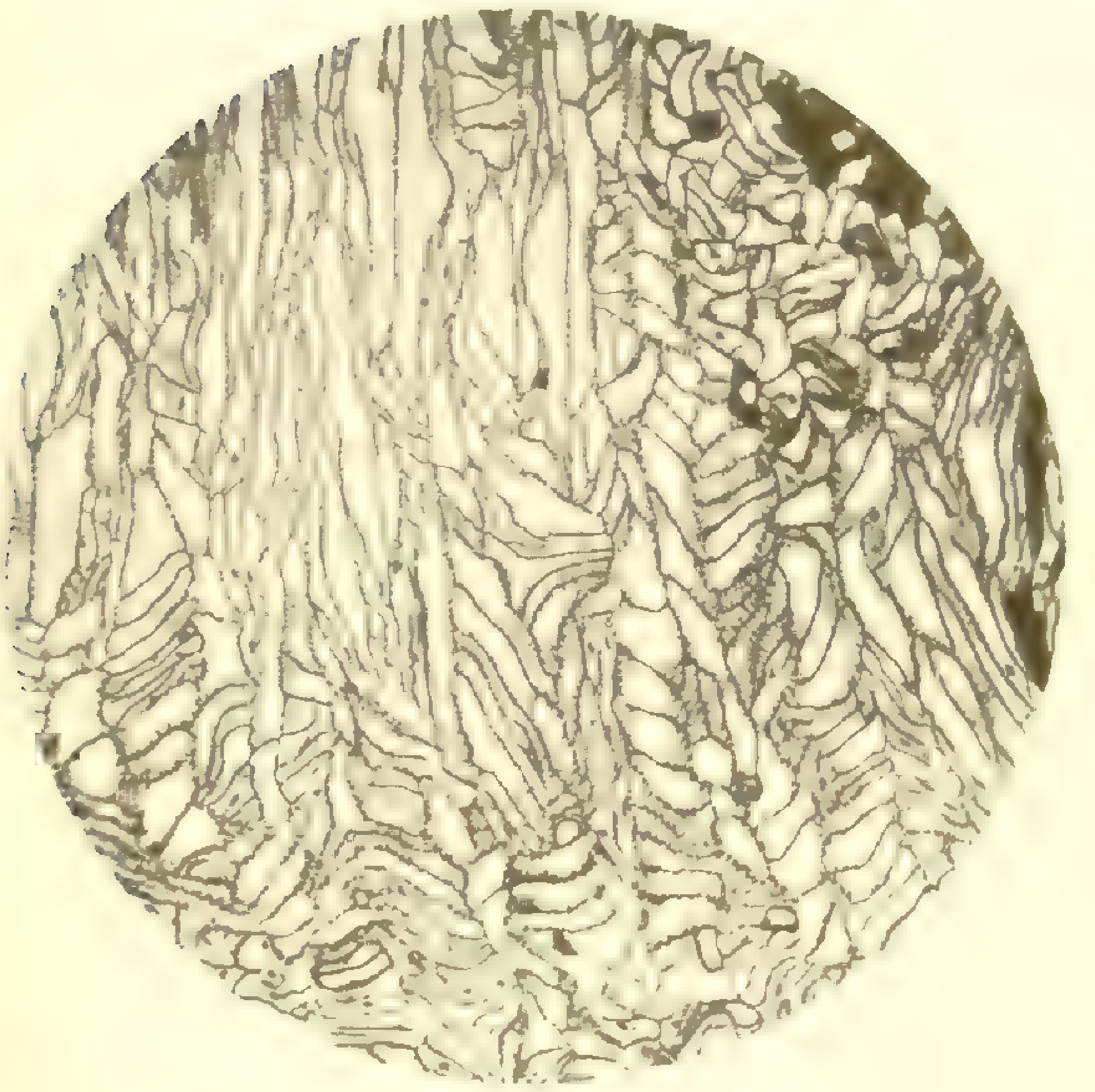

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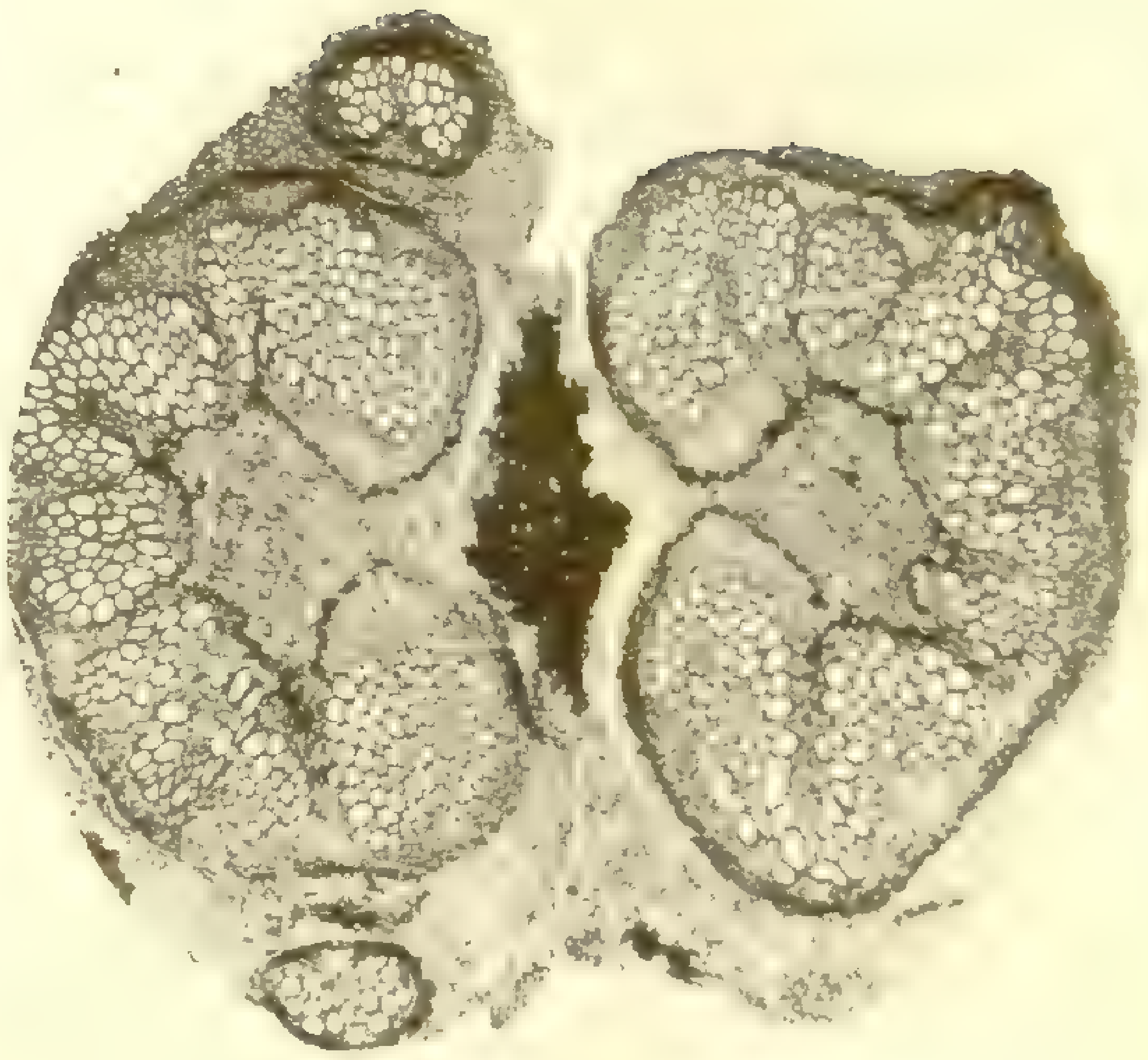

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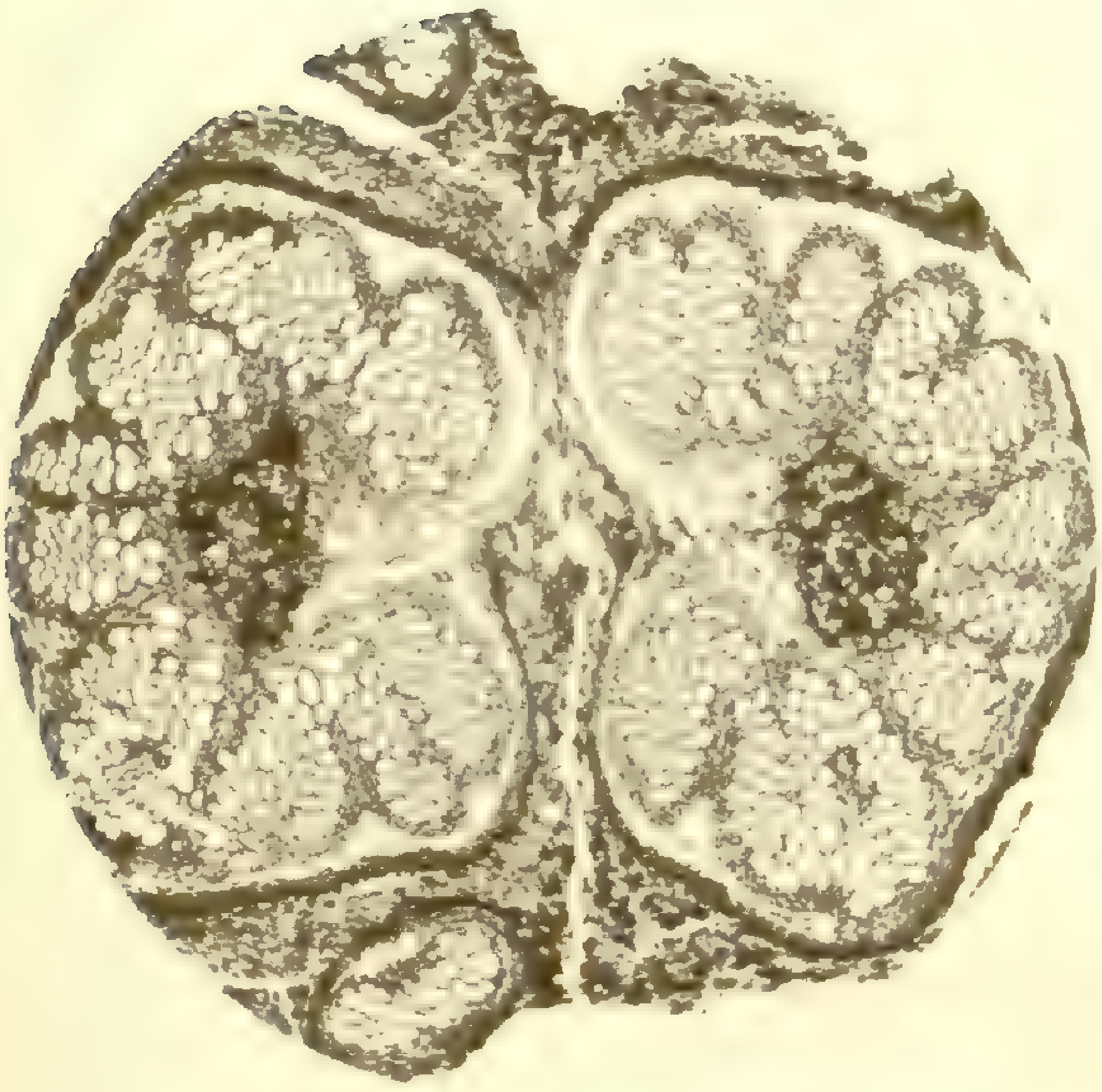

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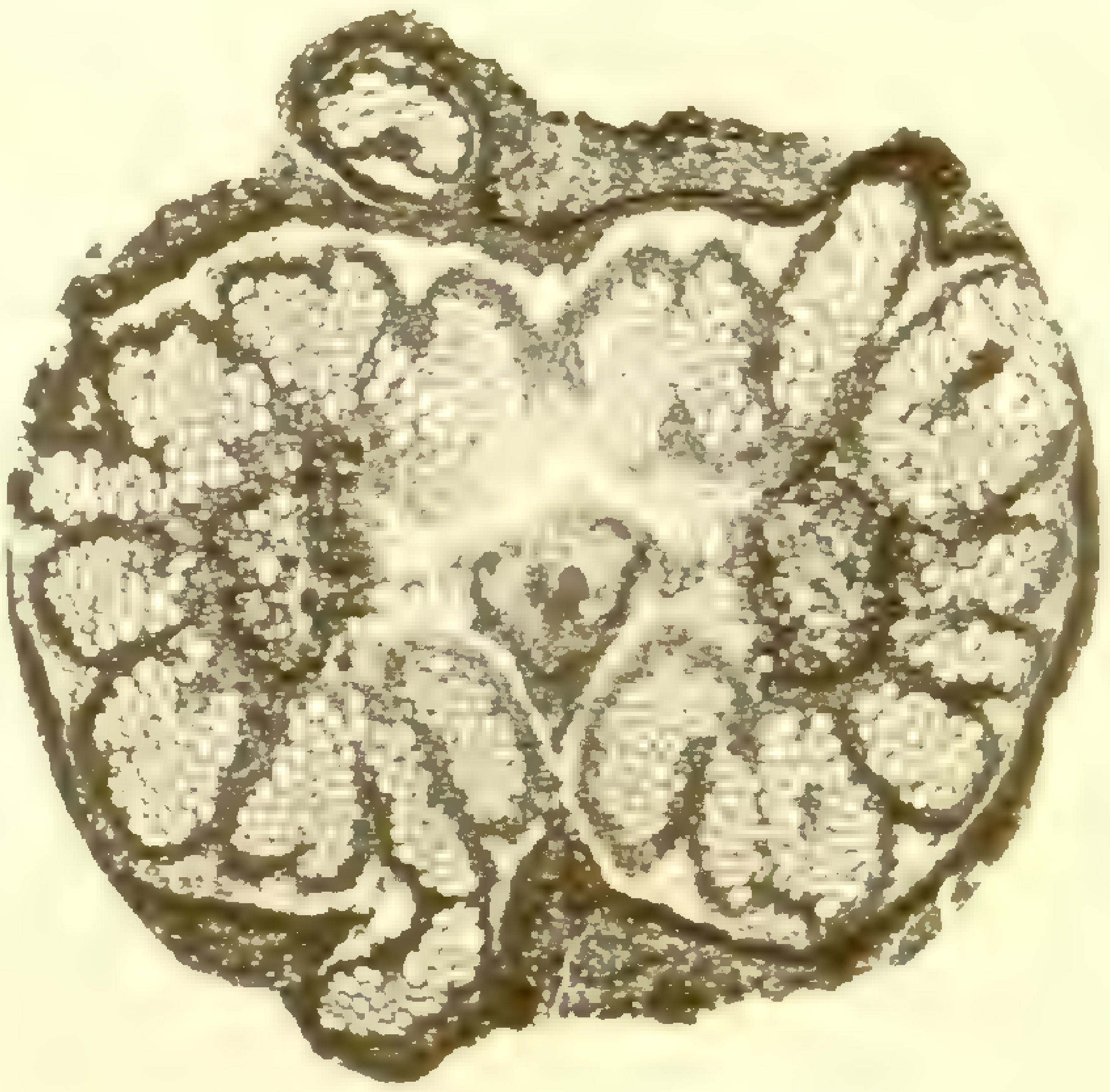

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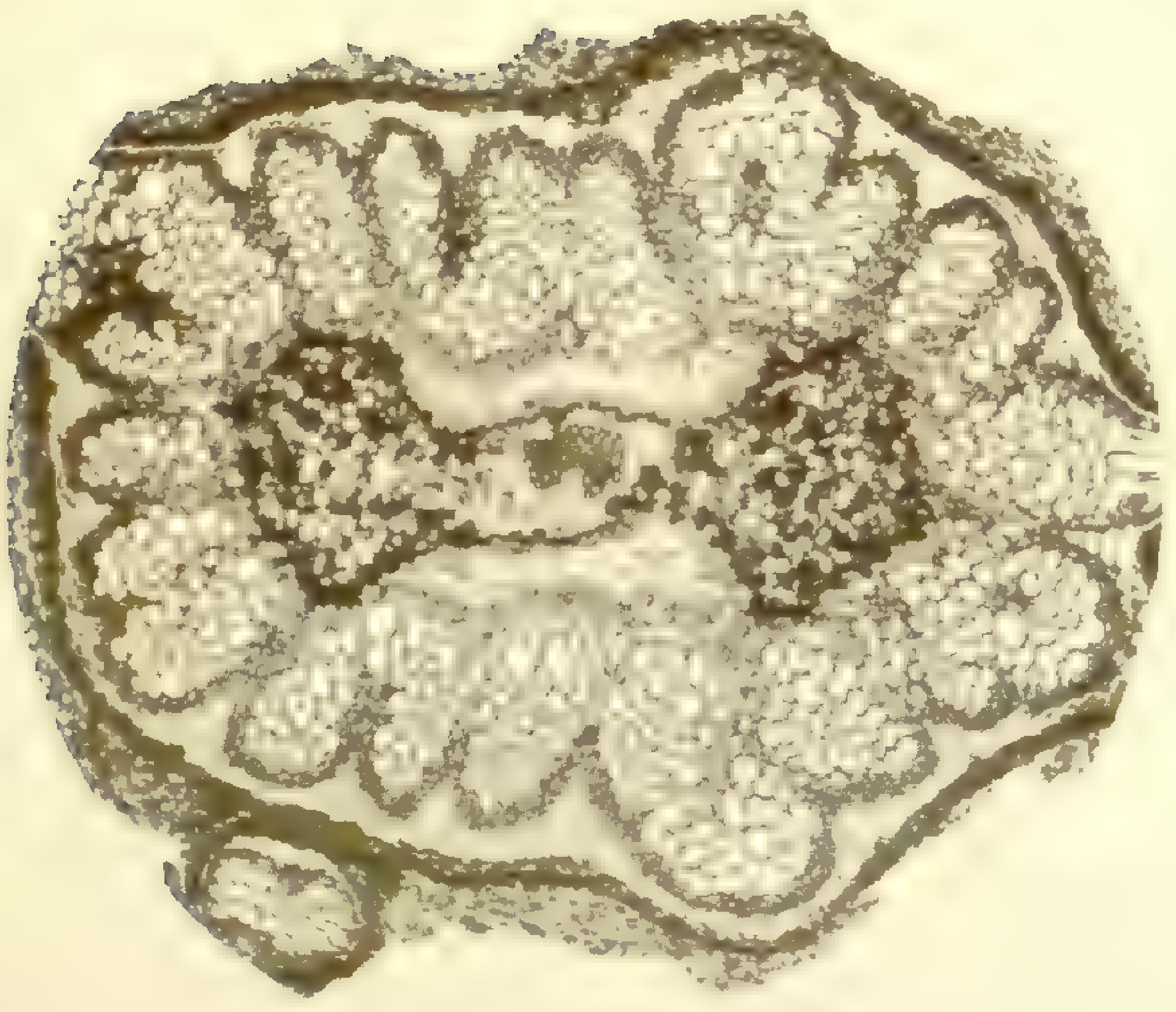

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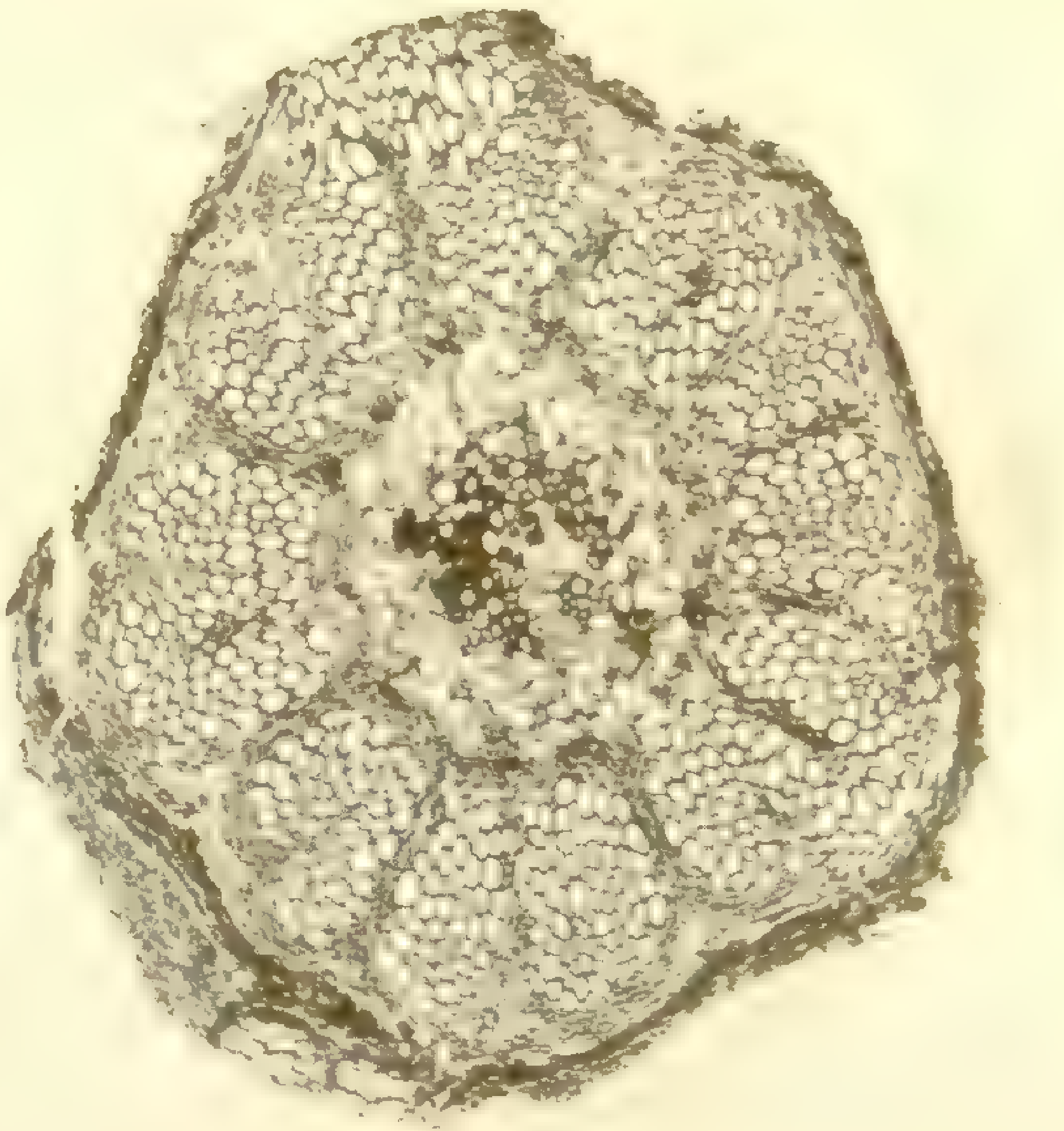

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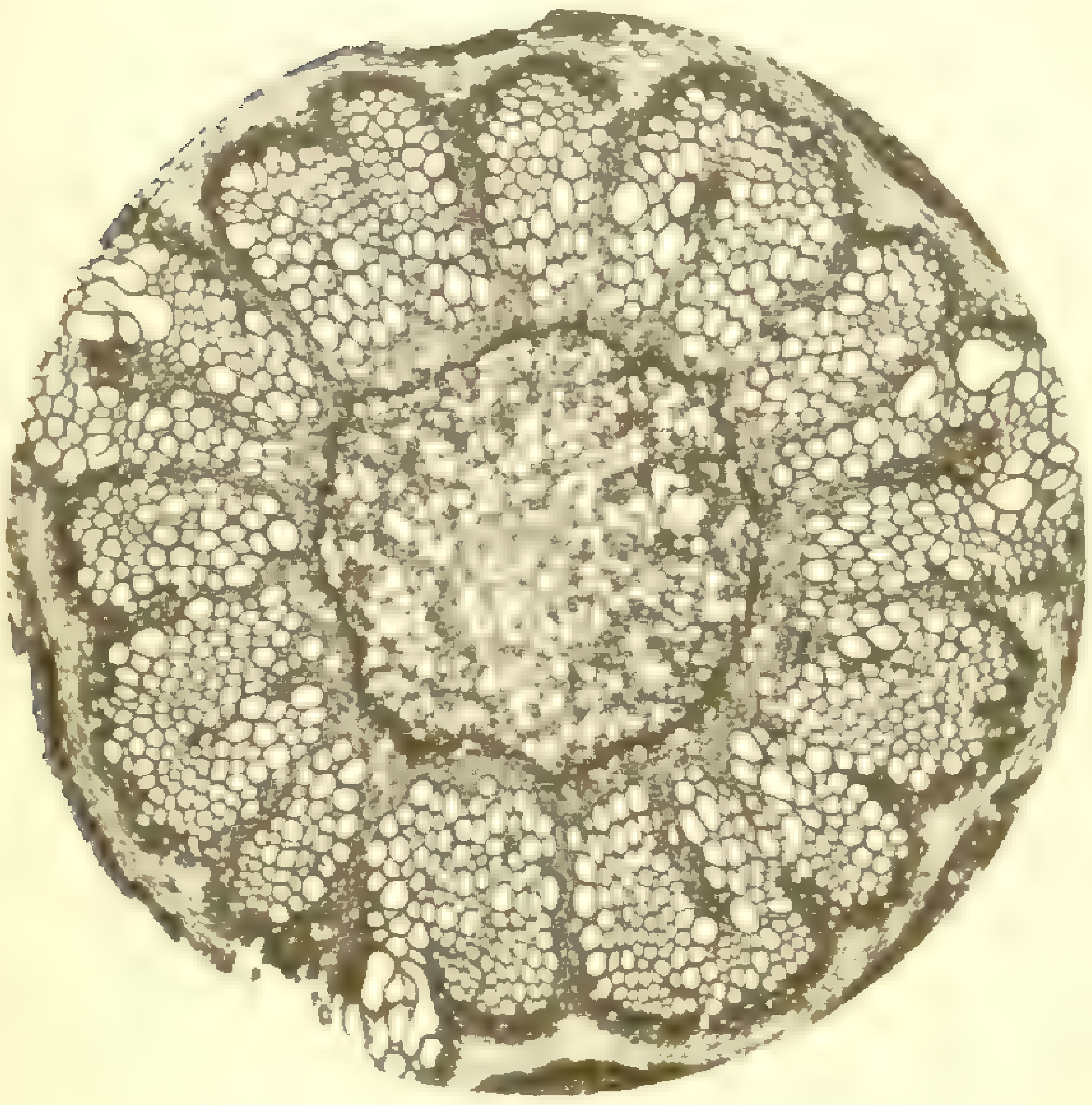

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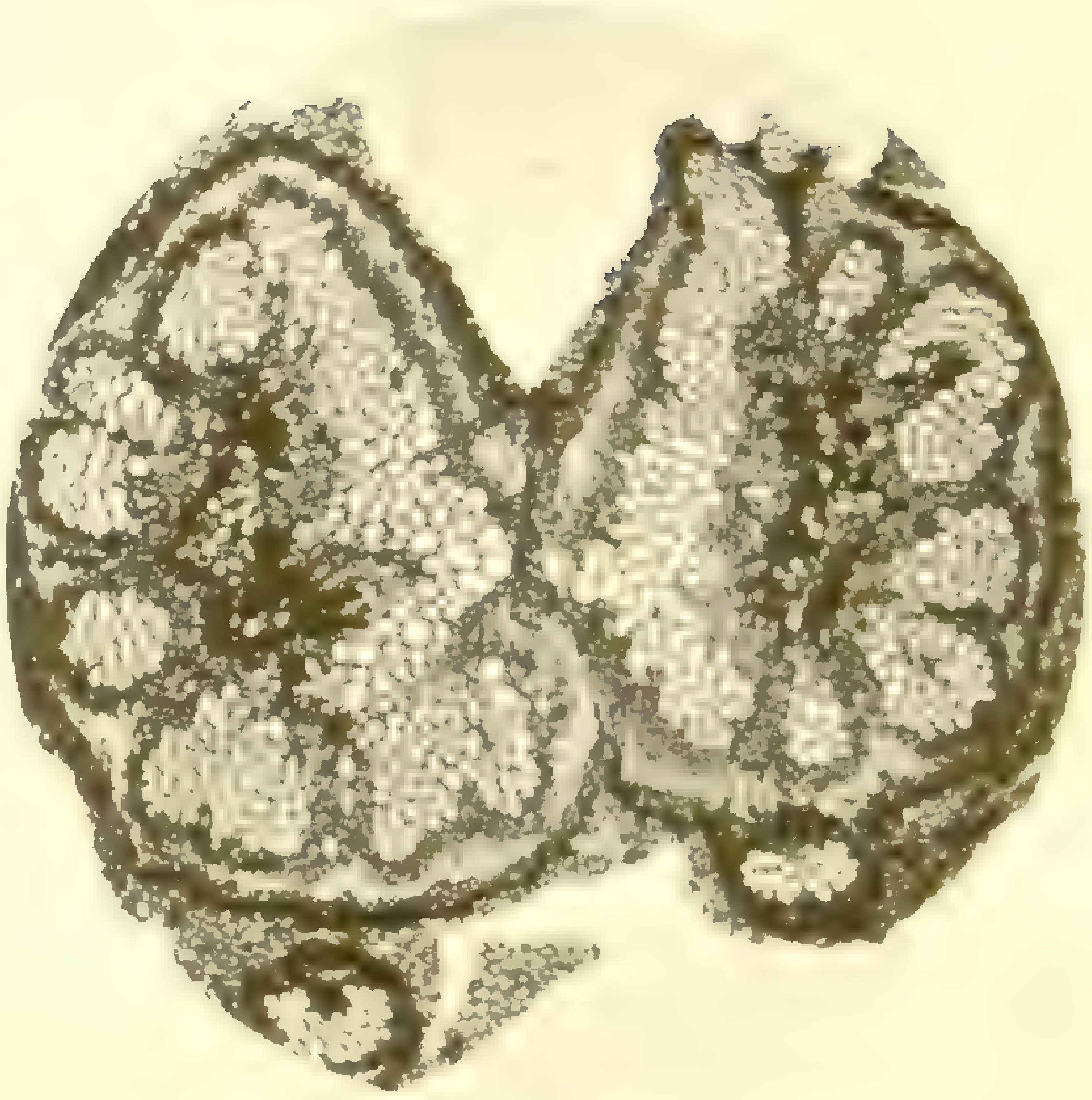

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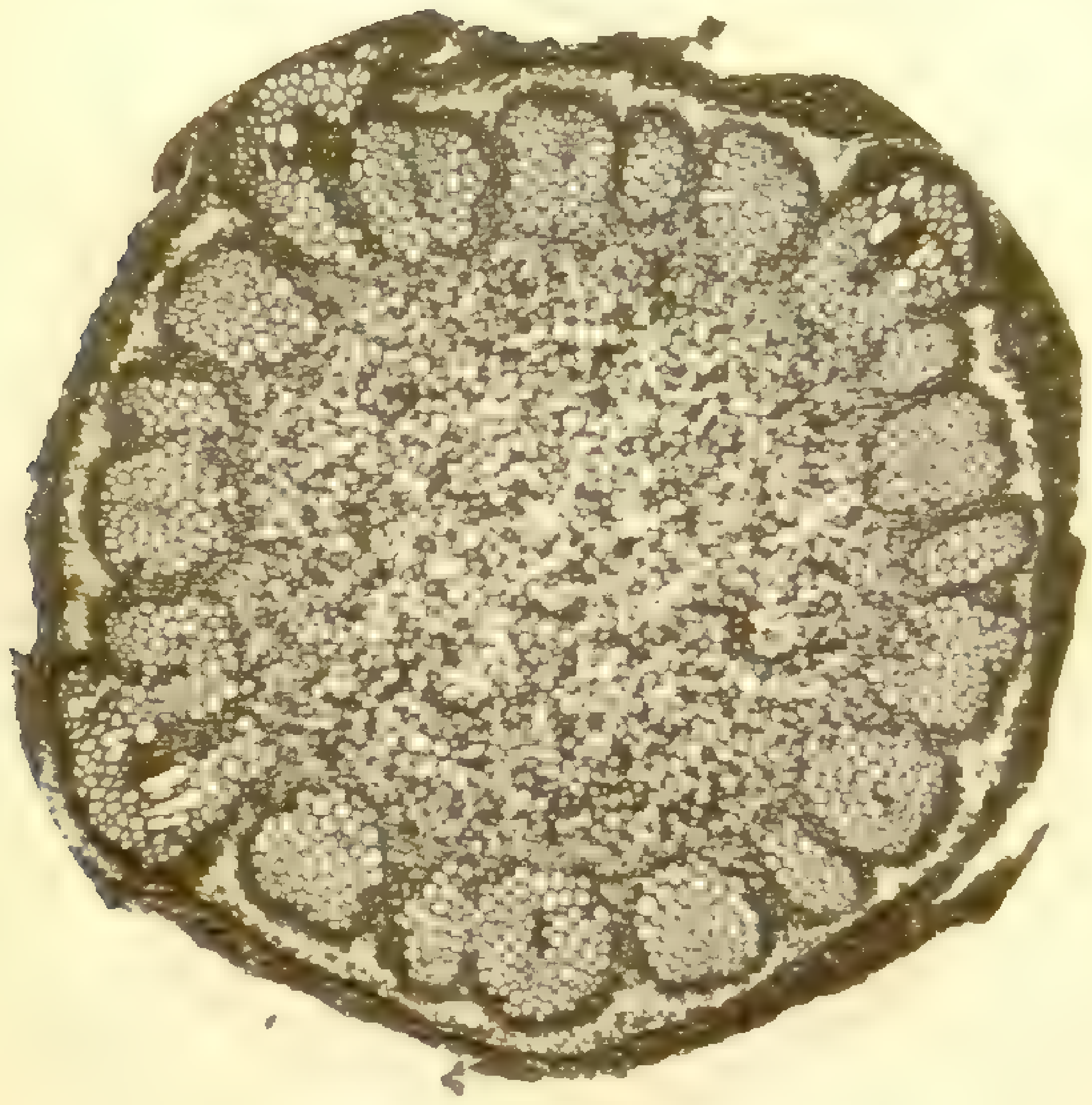

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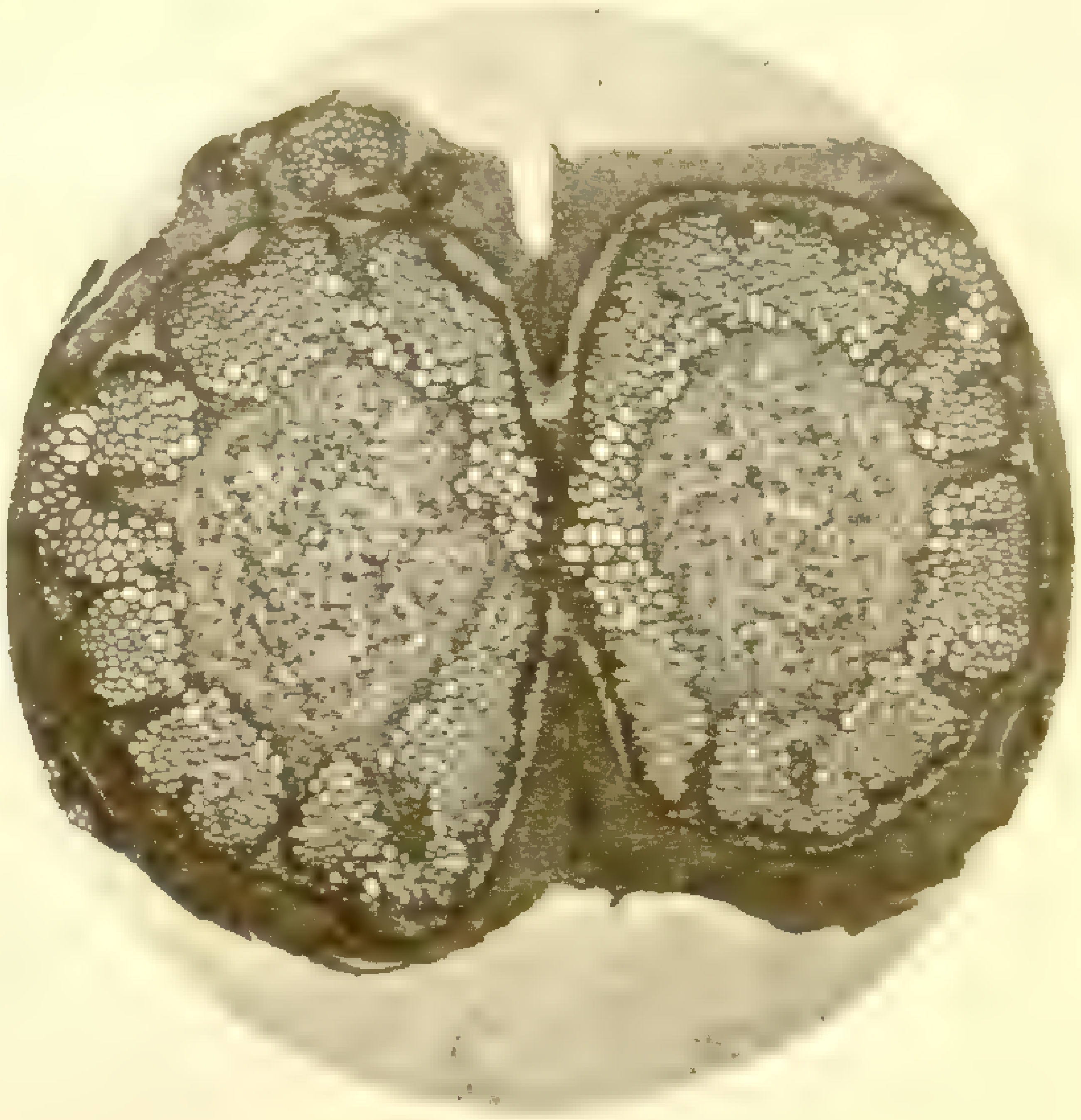

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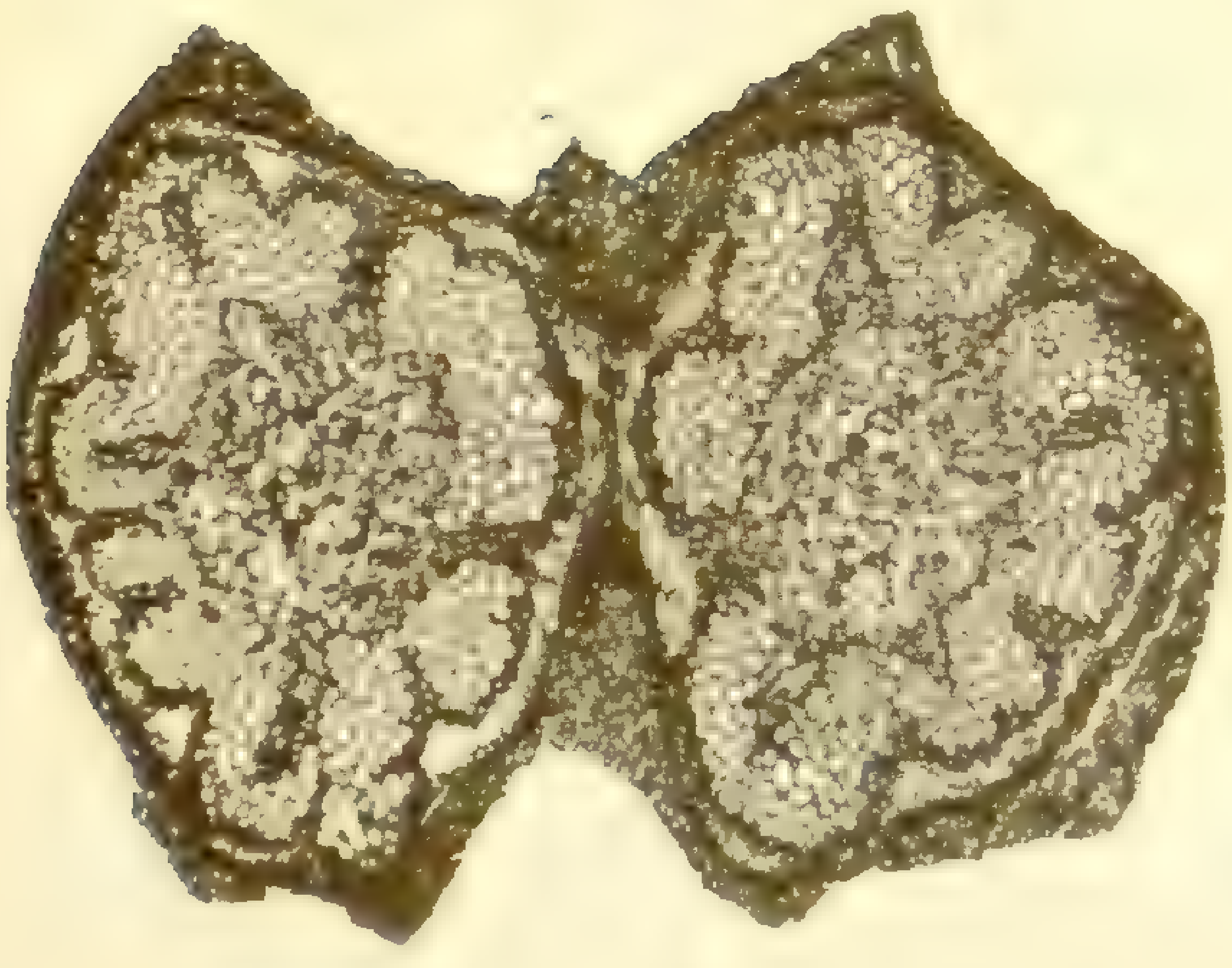

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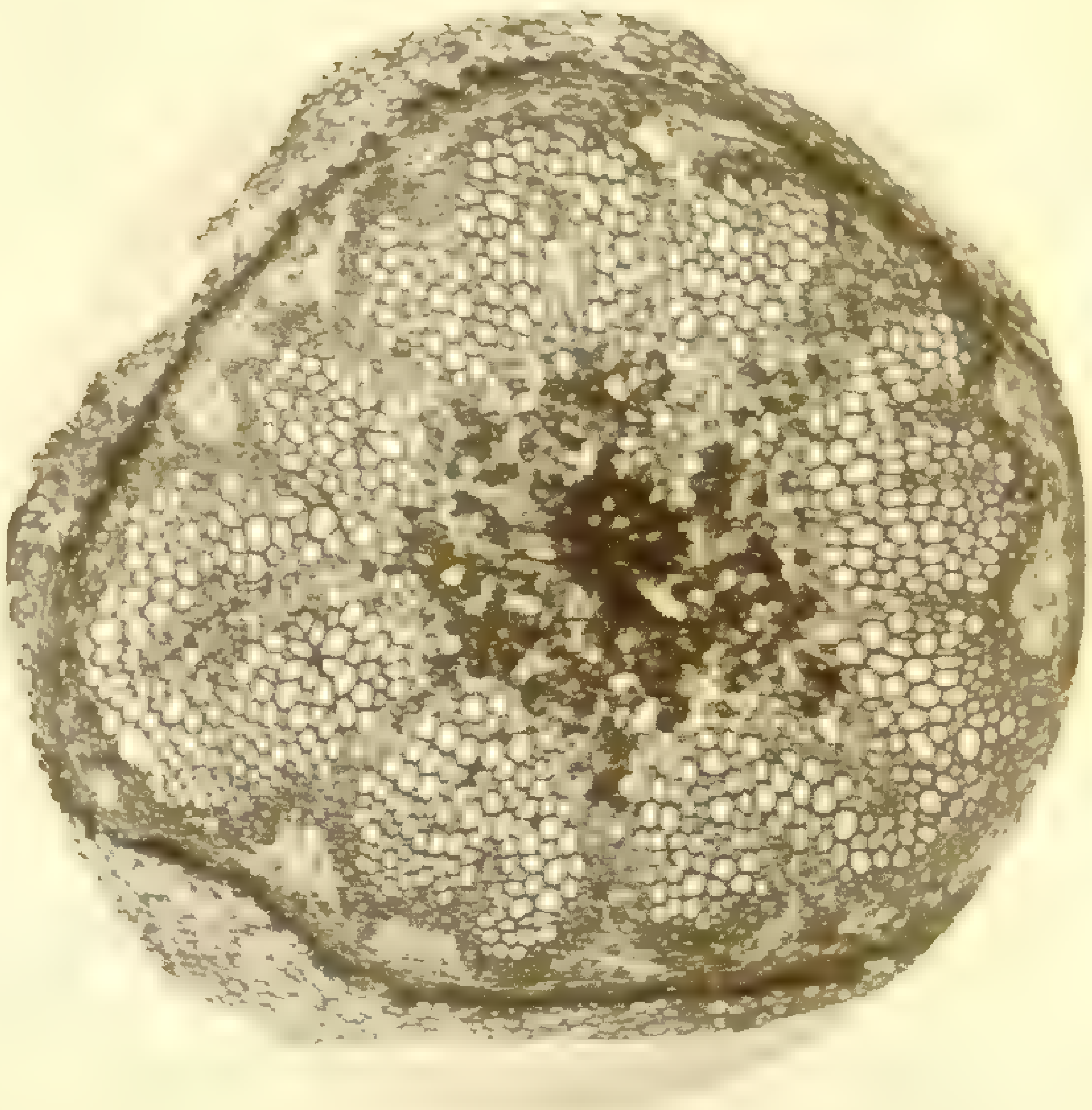

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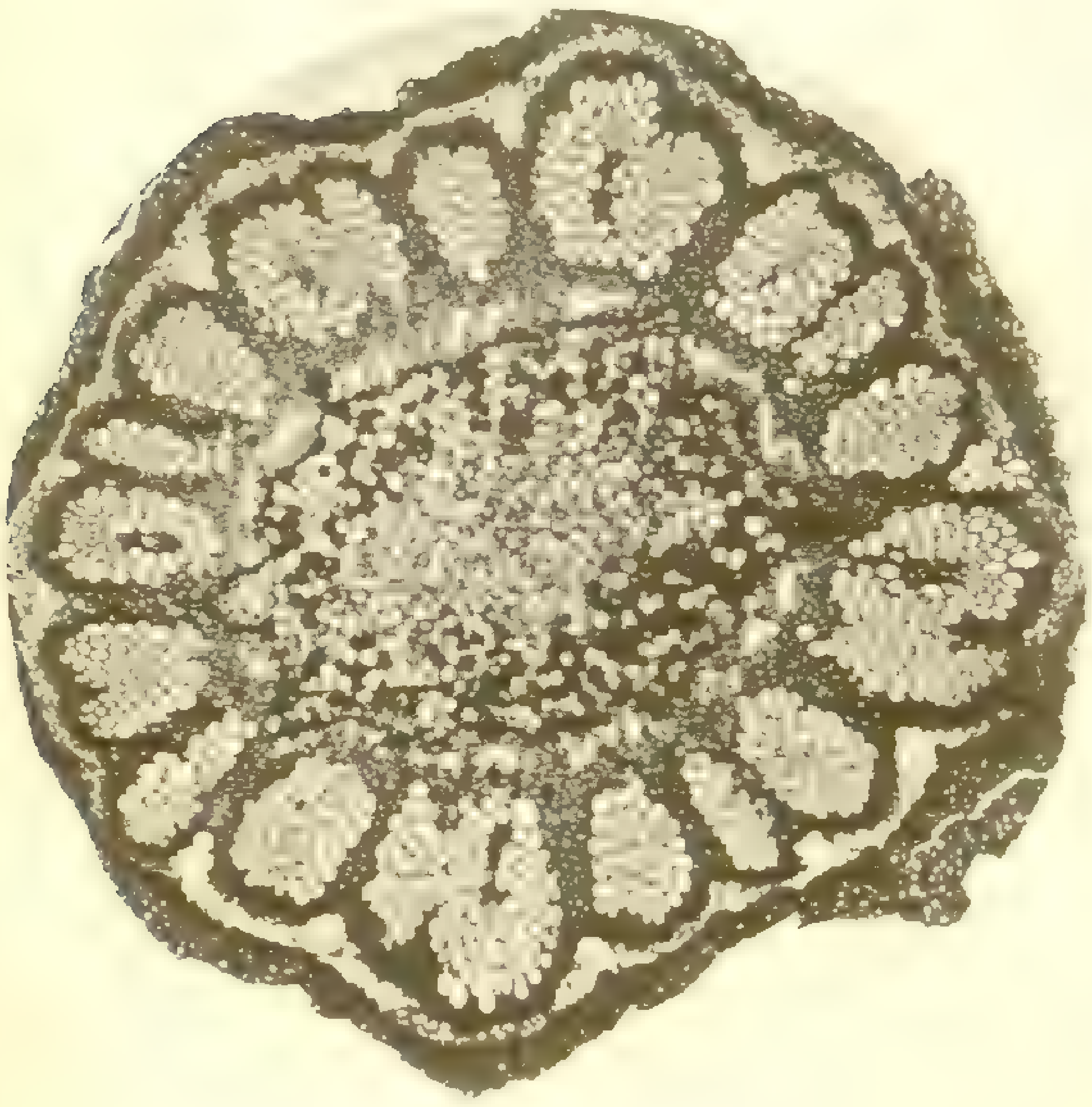

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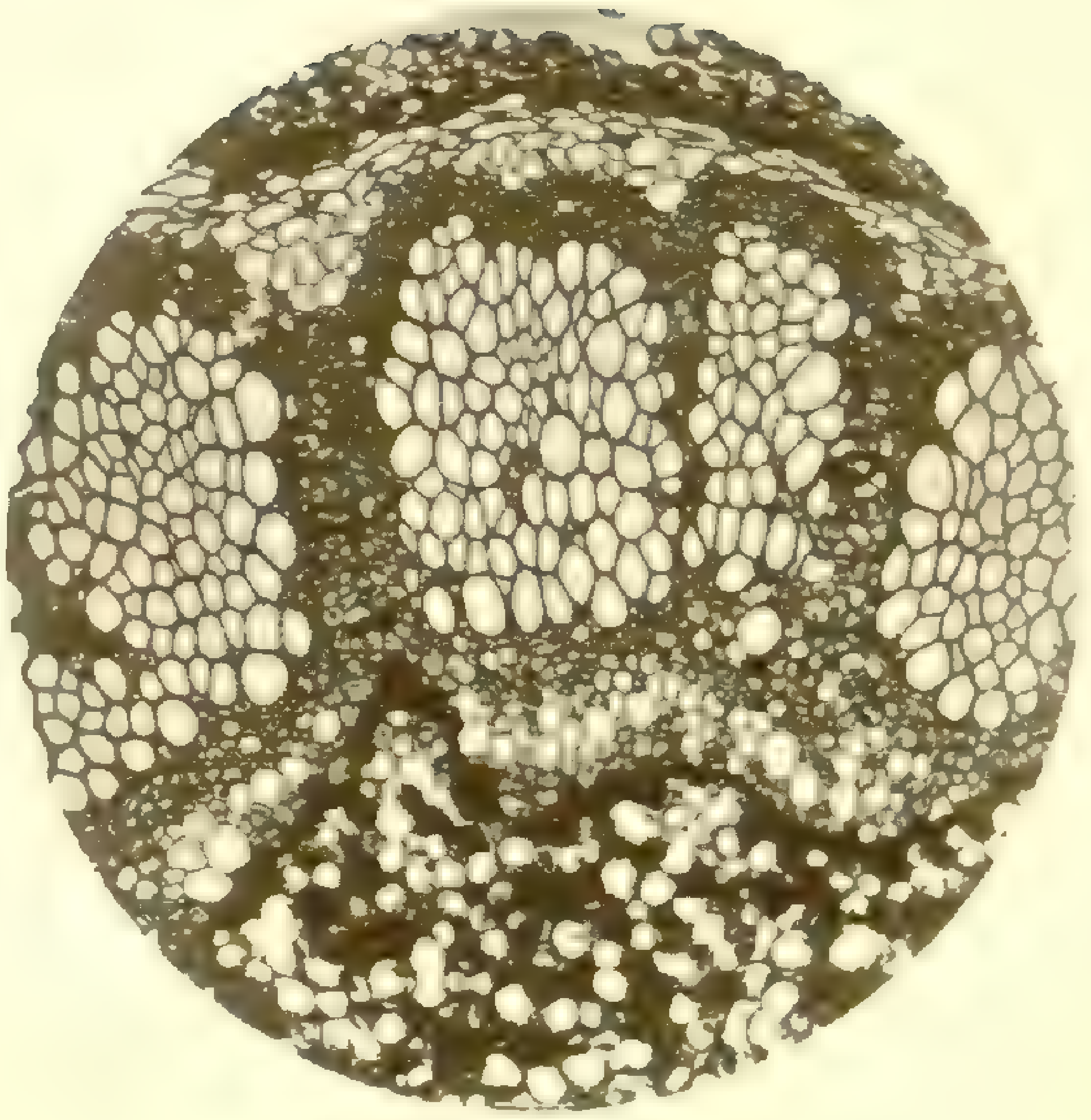

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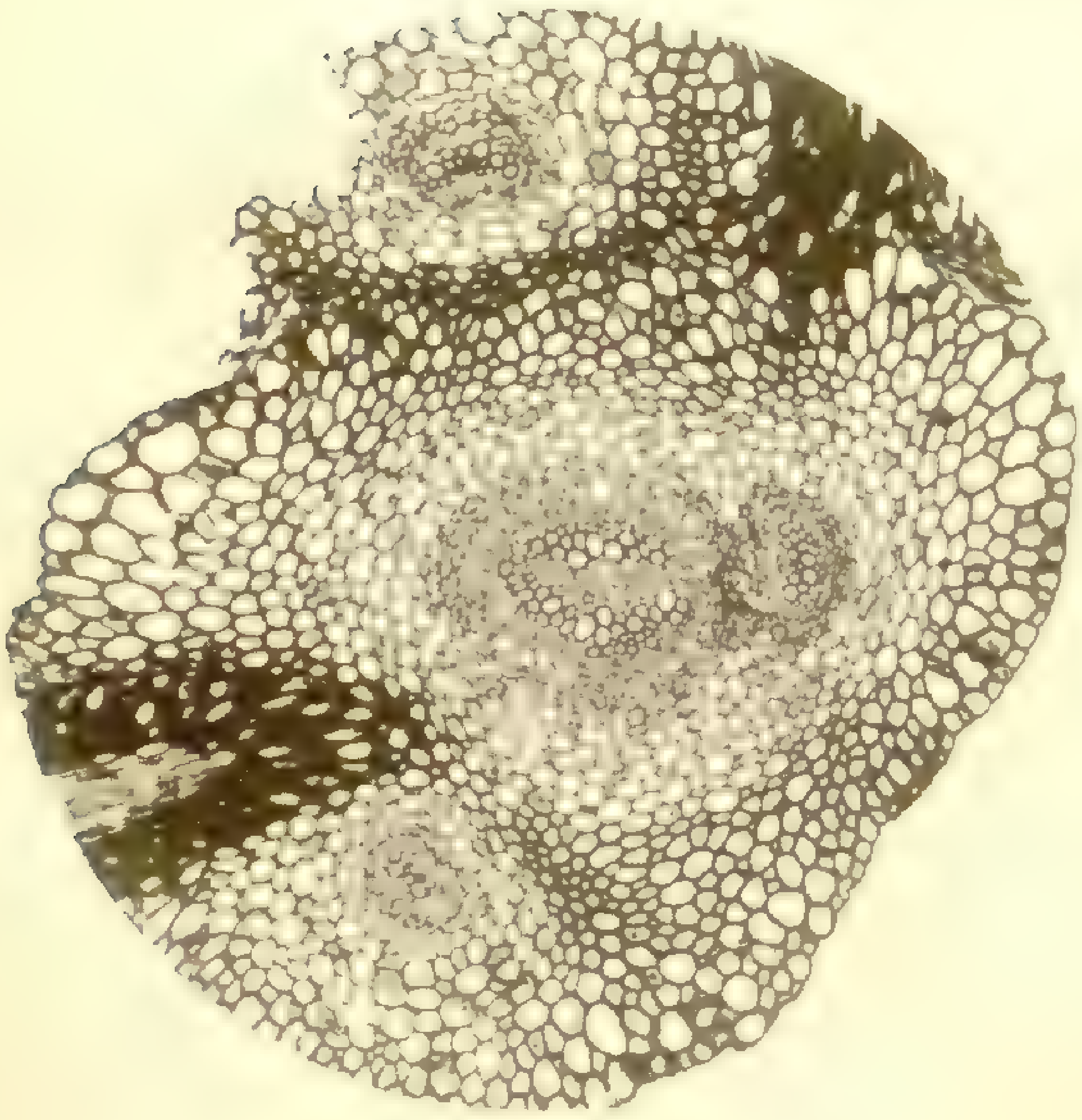

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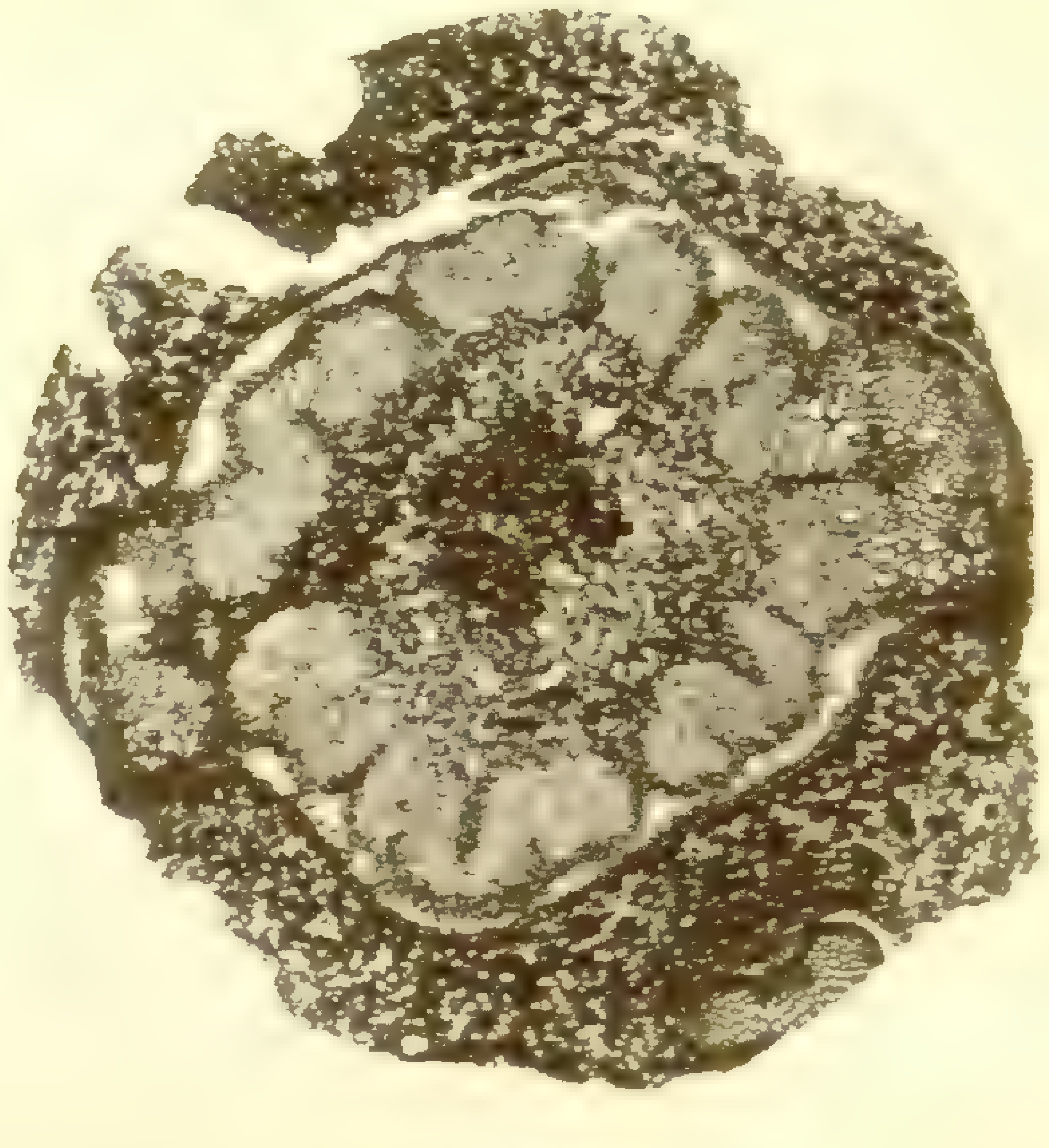

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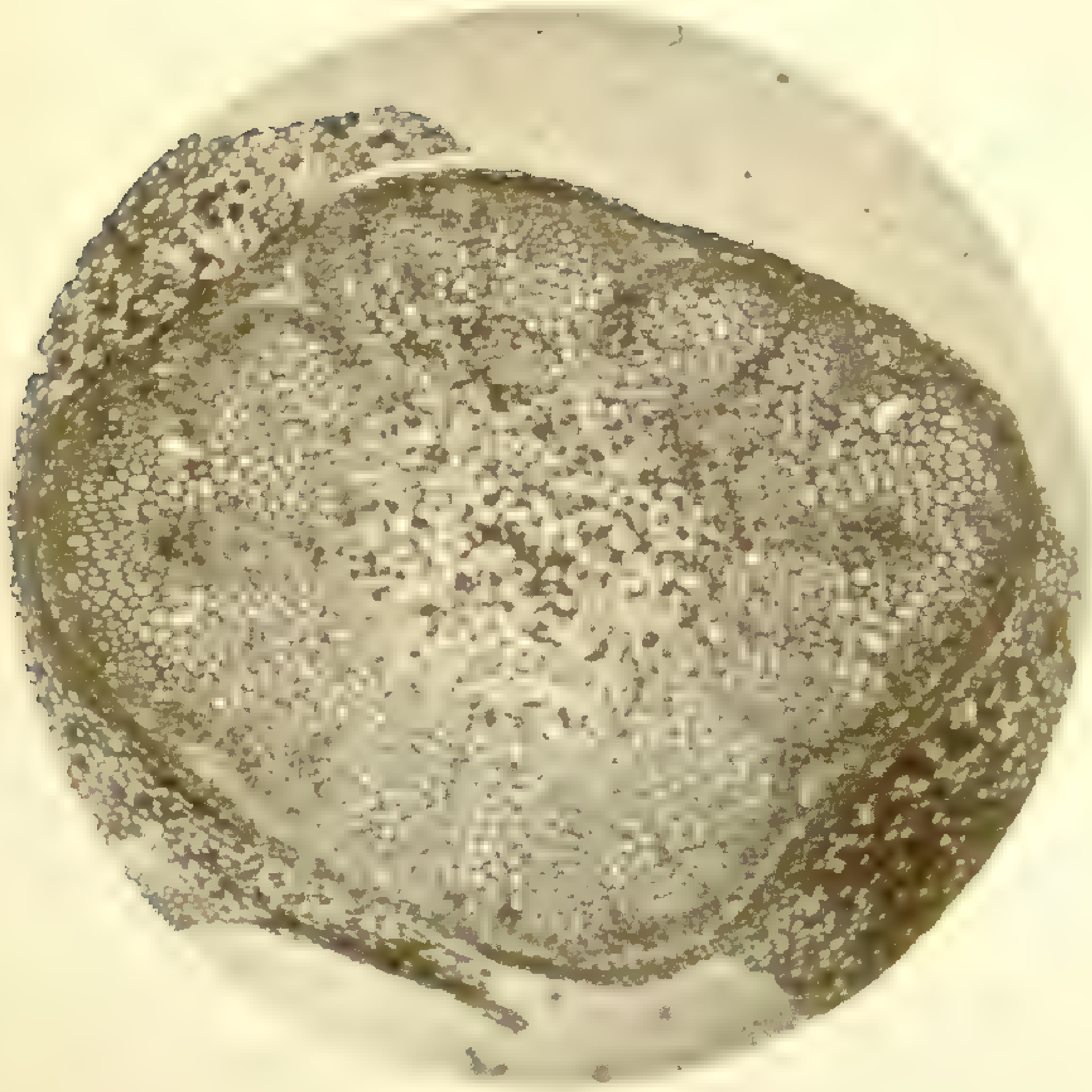

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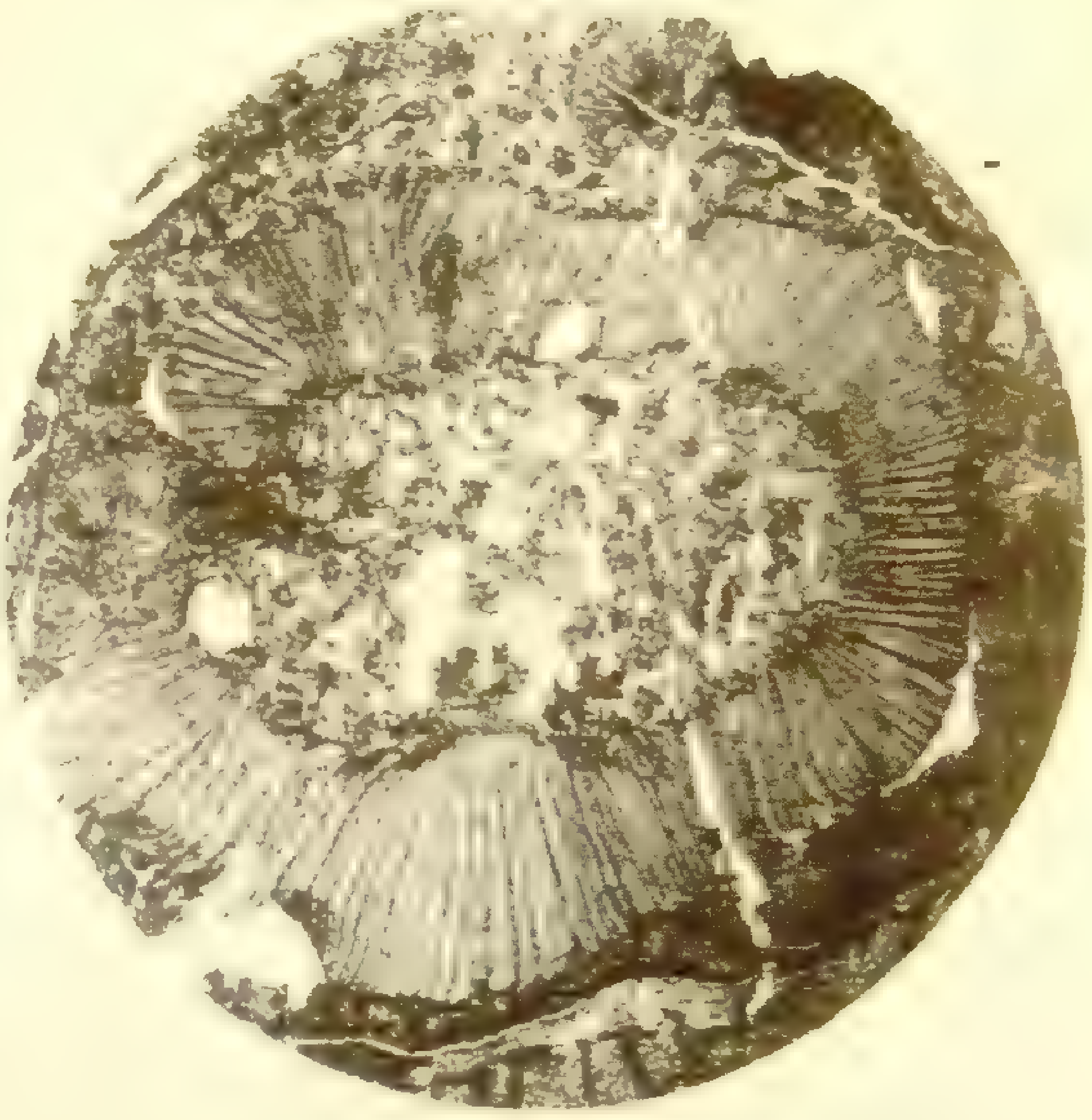

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FAULL on OSMUNDACEAE.

BRIEFER ARTICLES.

SOME ERRONEOUS REFERENCES.

In 1794 C. H. Persoon published in Roemer's *Neues Magazin für die Botanik* an important article that seems to have been almost entirely overlooked. It begins on page 63 under the title, *Neuer Versuch einer systematischen Eintheilung der Schwämme*, and is continued, pages 81–128, as *Dispositio Methodica Fungorum*, with four plates. This latter part was reprinted and considerably extended in 1797 as *Tentamen Dispositionis Methodicae Fungorum*. This work, from pages 1 to 48, is an exact copy of the 1794 article, so that anyone possessing the *Tentamen* can give the correct reference to the original publication by simply adding 80 to the page number of any of the first 48 pages. The parts in the 1797 work that are new are the title-page, preface, and pages 49 to 76. The plates are the same.

References for original descriptions in the main part of the *Tentamen* should therefore be made to the 1794 paper instead. For *Puccinia graminis* and *P. Circaeae*, instead of 1797, as always given, the correct date is 1794, which is also the date of the original description of the genus *Uredo*, instead of 1795 as given in Saccardo's *Sylloge Fungorum* and in Pfeiffer's *Nomenclator Botanicus*.

C. H. Persoon also contributed ten species of Aecidium to Gmelin's edition of Linne, *Syst. Nat.* 1791, and his name follows the descriptions. So we should write, for example, *Aecidium Euphorbiae* Pers.; not *Aecidium Euphorbiae* Gmel. In Usteri's *Annalen der Botanik* for 1796, pt. 19, p. 43, Persoon speaks of having contributed to Gmelin's edition of this work. The date of these species is sometimes given as 1796, which comes from reference to Gmelin's edition of Linne, *Syst. Veg.*, a work that is identical page for page, so far as the volume containing the fungi is concerned, with the earlier *Syst. Nat.*, except in the title-page.

In *Hist. Fisica y Politica de Chile* 8 : 43, 1852, Montagne describes *Puccinia Malvacearum* Bertero, not *P. Malvacearum* Mont. as always written. That Montagne intended this is shown by his adding: "Solo me pertenecen el diagnosis y la descripcion."

In his *Flora Fernandesiana* 10. 1835, Montagne also writes *Uredo Cestri* Bertero and *Uredo Hydrocotyles* Bertero, not Montagne as quoted in references to the work.—E. W. D. HOLWAY, *Decorah, Iowa.*

PUCCINIA INANIPES.

THROUGH some error the description of this species (BOT. GAZ. **31**: 332. 1901) is incomplete. It should be:

Puccinia inanipes Diet. & Holw., n. sp.—Sori on both sides of the leaf, particularly on the upper, scattered, punctiform; uredosori brown; uredospores elliptical, brown, echinulate, 25–30 × 20–25μ; teleutosori black; teleutospores broadly elliptical, rounded at both ends, and when dry with both ends depressed, scarcely constricted, apex with a very slight cucullate thickening, smooth, dark chestnut-brown, 34–42 × 28–31μ, with long hyaline hollow pedicels which easily break at the base from the host plant.

On *Eupatorium brevipes*, Oaxaca, Oct. 18, 1899, no. 3677.—E. W. D. HOLWAY, *Decorah, Iowa.*

THE POSITION OF PLEUROCOCCUS AND MOSSES ON TREES.

HAVING observed during the past winter that certain chlorophyll-containing plants do not grow most abundantly on the north side of trees, as is commonly supposed by the laity at least, and as stated in at least one of the more recent books on botany, the author herewith presents some of the results of his observations, which are still in progress.

The trees on which the observations were made were located in a piece of woodland and were principally black oaks with a few white oaks, chestnuts, and beeches. The chlorophyll-containing plants found growing upon these trees were principally pleurococcus and some members of the Bryaceae. These were growing upon all sides on the bark of the trees except the southwest side, and approximately in the following ratio: In 10 per cent. of the trees upon the west side; in 10 per cent. upon the northwest side; in 10 per cent. upon the north side; in 20 per cent. upon the northeast side; in 35 per cent. upon the east side; and in 15 per cent. upon the southeast side.

A further examination showed that they grew in the greatest profusion on the shelving side of the trunks of trees with a slant of 10° to 20°; furthermore trunks which were nearly vertical were not inhabited by these minute plant forms. They were, however, nearly always found upon the slanting surfaces near the ground. In some cases the growth extended approximately to a height of 20 or 30 feet, and the position varied as the shelving varied, so that the growth might extend on the same tree at different heights from 90° to 270°.

Rather careful observations thus far obtained tend to show that it is the shelving portions of the trunks of trees which receive and hold the greatest amount of moisture, and as the latter is apparently one of the most important requisites for the development of these green plants, we can readily understand why we find them distributed on nearly all sides of the trees, and not limited, as popularly supposed, to the north side of trees only.— HENRY KRAEMER, *Philadelphia*, *Pa.*

CONTRIBUTIONS TO THE KNOWLEDGE OF THE PHYSIOLOGY OF KARYOKINESIS.[1]

(WITH ONE FIGURE)

THE investigations, concerning which this is a preliminary report, were undertaken to throw more light upon the subject of the physiology of karyokinesis, a subject which has not received attention commensurate with its importance. This paper presents only the results regarding the relationship of light of various wave-lengths to the rapidity of mitotic nuclear division. The investigations were undertaken at the suggestion of Dr. E. Mead Wilcox and were completed under his direction. I take this opportunity to offer him my sincere thanks for constant and helpful suggestions throughout the course of the investigations.

The roots of *Allium Cepa* were selected as affording the most convenient and suitable objects for the experiments. Bulbs of uniform medium size were selected with great care in the local markets. These bulbs were placed over suitable vessels in such a position that the base of the bulb barely touched the pure water with which the vessels were filled. The usual adventitious roots soon formed, and these were allowed to attain a length of about one centimeter before the bulb was transferred to the light cages as hereinafter explained.

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[1] Contribution from the Botanical Laboratory of the Oklahoma Agricultural and Mechanical College. I. Abstract of thesis.

For the purpose of securing light of various wave-lengths, use was made of the usual double walled bell glasses prepared as follows: The first bell glass was filled with pure water and the second one was painted with a very thick coat of lampblack. Two other bell glasses were filled with solutions *A* and *B* respectively. Solution *A* was made by adding to a 0.06 *n* solution of copper sulfate ammonia until the precipitate ceased to form. Solution *B* consisted of 0.05 *n* solution of potassium bichromate.

For each of the experiments there were selected bulbs having roots at least one centimeter in length, and as many of these as possible were placed under each of the bell glasses prepared as above. The bulbs were then left under these glasses, so arranged as to allow of the normal respiration taking place, for between two and three days before the beginning of the experiment. Roots were then collected from the bulbs under each of the glasses at intervals of four hours during the twenty-four hours of the day. The tips of the roots thus secured were killed in the usual chrom-acetic-acid fixing mixture and imbedded in paraffin according to the usual method. The sections were cut 13.3μ thick and stained according to Heidenhain's iron-alum-haematoxylin method.[2]

By means of a very simple method, devised during the investigation, it was then possible to count accurately the number of nuclei in the process of division and the number resting. A uniform combination of ocular, tube length, and objective were used throughout the work. In each case the slide was so adjusted as to include in the field nearly all the portion of the root tip lying back of the apical cells, the field being so placed as to include these apical cells. Within this field thus selected it was a relatively simple matter to make very accurate counts of the dividing and resting nuclei. Nuclei were classed as dividing from the first indication of segregation of the chromatic matter in the prophase to the formation of the daughter nuclei at the close of the telophase.

The following tabulation shows the results thus far secured by the use of the above described methods applied to this investigation. Each percentage as given represents the average of nine counts made on three sections taken from each of three roots, each of the three roots used being taken from a different bulb under similar conditions. It seems therefore that the results secured are representative and trustworthy. The percentages are in all case the proportion of nuclei found dividing.

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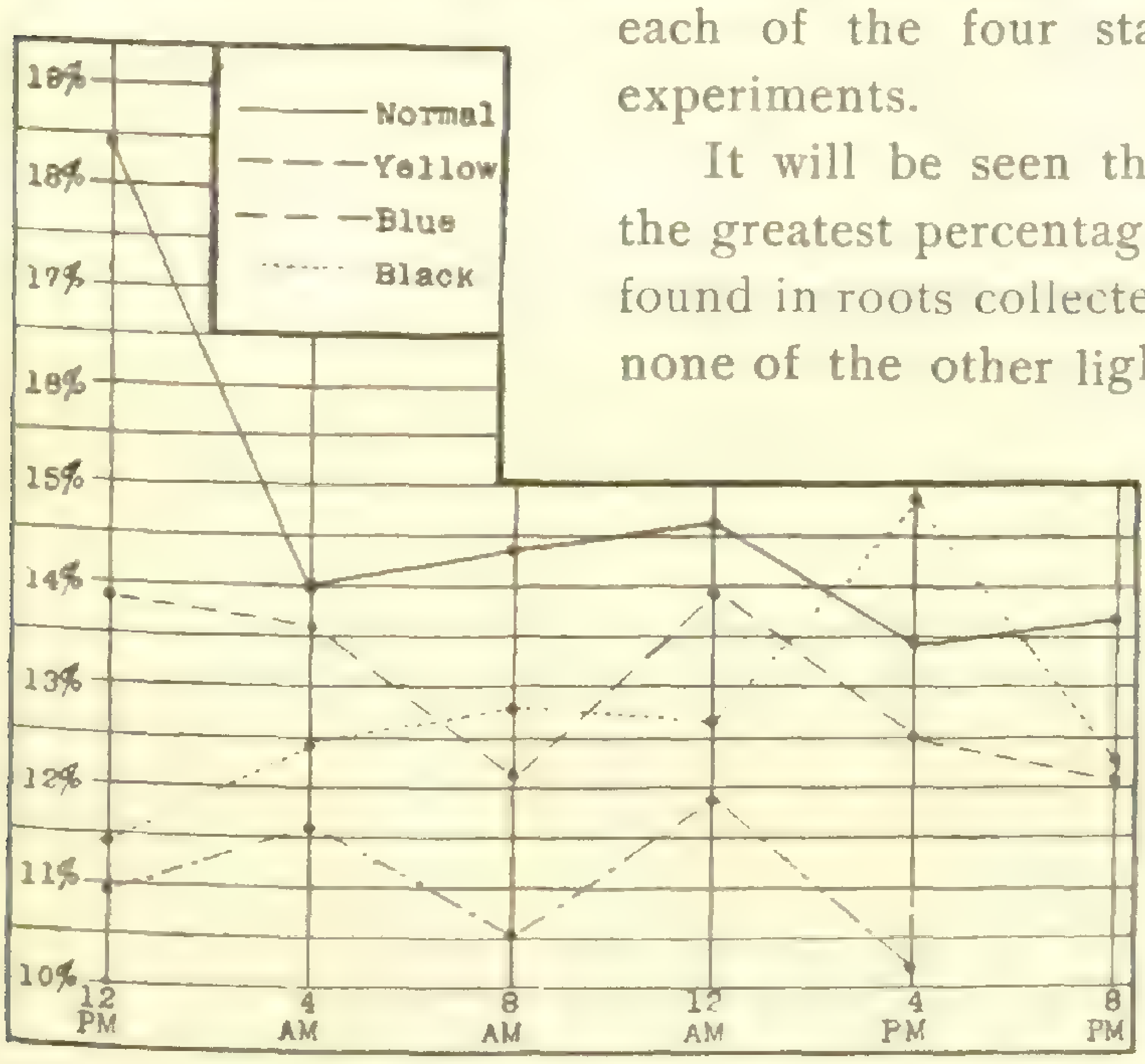
[2] LEE, A. B.: The microtomist's vade-mecum 175–176. 1896. [4th ed.]

Time	Normal	Yellow	Blue	Black
12 P. M.	18.3 %	13.8 %	10.9 %	11.4 %
4 A. M.	14.0	13.6	11.6	12.4
8 A. M.	14.3	12.1	10.5	12.7
12 A. M.	14.6	13.9	11.8	12.6
4 P. M.	13.4	12.5	10.2	14.8
8 P. M.	13.6	12.1	....	12.3
Averages	14.7 %	12.6 %	11.0 %	12.7 %

In the accompanying figure these same results are represented in the form of curves showing the percentage of dividing nuclei under each of the four stated conditions of the experiments.



It will be seen that in the normal light the greatest percentage of dividing nuclei was found in roots collected at midnight, while in none of the other lights does this same relationship hold true. In the roots grown in darkness there was found the lowest percentage of dividing nuclei, at midnight, and the highest percentage is found at 4:00 P.M.

Future studies must determine if this same relation, as exhibited in the curves shown, exists in cells having active chloroplastids during normal photosynthesis. Studies of this type are now under way, and further discussion of this subject is reserved until the completion of the investigations mentioned.—ARTHUR CARR LEWIS, *Agricultural and Mechanical College, Stillwater, Oklahoma.*

CURRENT LITERATURE.

BOOK REVIEWS.

Britton's manual.[1]

SUCH will probably be the familiar designation of a book that covers the area so long known as that of Gray's *Manual*. It is a book that has long been waited for, since it puts into sharp contrast the two extreme views concerning species and nomenclature. So long as the conservative position in reference to these matters was represented by the only handy manual of our best known region it was immensely strengthened, since it did the chief training in the use of manuals. Now, however, the issue is squarely joined, and both views will get that support which comes from usage. It seems to the reviewer, therefore, that some arguments heretofore used against the so-called radical views will disappear, and that the real test of usage can now be applied to both positions.

The position of Professor Britton as to species and nomenclature is too well known to need explanation. For the first time, we have a manual presentation of the idea of species applied to the ultimate recognizable segregates of plants. It is now to be tested whether those of ordinary training and experience can determine species in this new sense, or whether the use of a manual must now pass out of the reach of amateurs and be restricted to specialists. For example, can an amateur distinguish the 43 species of Viola found in Britton's *Manual* as he can 18 species found in Gray's *Manual*; or the 13 species of Sisyrinchium and the 15 species of Antennaria found in the former, as he can the two and one species of the latter? This is not intended as the slightest criticism of the work of segregation now going on, much of which is undoubtedly necessary; but it is raising the question whether the use of manuals is not hereafter to be very much restricted. It undoubtedly will remove them from elementary botanical courses, which at least will be a valuable service.

For the first time, also, there is a manual presentation of the so-called reform nomenclature, and the new names will now have a chance to become as familiar as the old. So long as they appeared only in journals and monographs and bulky volumes there was no chance for popular usage, and their unfamiliarity always scored a point against them. There could be no wiser move towards setting the reform nomenclature upon its feet than the preparation of a handy manual which presents it, provided, of course, that this same manual makes it possible for the great host of amateurs to determine their plants with satisfaction.

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[1] BRITTON, NATHANIEL LORD: Manual of the flora of the northern states and Canada. 8vo. pp. x+1080. New York: Henry Holt and Company. 1901. $2.25.

Concerning the other features of this *Manual* there can be no real discussion. The Engler and Prantl sequence is a matter of course, and is not under discussion as contrasted with that used in Gray's *Manual*. The use of the metric system is another well approved step which calls for no special comment, except that our manuals have been too slow in adopting it.

As to the work of the publishers, it deserves very high praise. Thin but tough paper, clear type, and narrow margins, so that a book of over 1000 pages can be carried in a good-sized pocket and can be bought for $2.25 is a triumph of the publisher's art and common sense.—J. M. C.

MINOR NOTICES.

A MONOGRAPH of the North American Sordariaceae has been published by David Griffiths.[2] After a general discussion of distribution, methods, development, and spore dissemination, the six genera are presented as follows: Sordaria (13 spp., 5 new), Pleurage (31 spp., 13 new), Hypocopra (9 spp., 3 new), Delitschia (9 spp., 5 new), Sporormia (15 spp., 7 new), and Sporormiella (1 sp.). Material from over 20 states was studied, and the period of development of many of the species determined.—J. M. C.

ARTHUR H. CHURCH has begun the publication of studies "On the relation of phyllotaxis to mechanical laws." The first part[3] now before us deals with construction by orthogonal trajectories. A general historical discussion of phyllotaxy is followed by a record of observations accompanied by handsome half-tone illustrations representing chiefly high orthostichies. This is followed by discussions of the geometrical representation of growth, the application of spiral-vortex construction, ideal angles, and asymmetry.—J. M. C.

THE FOURTH PART of Engler's *Pflanzenreich* has appeared, and contains the Monimiaceae (family 101 of the spermatophyte series) by Janet Perkins and Ernst Gilg. After the usual discussion of the important structural features of the family, and its geographic distribution, there follows the systematic presentation. Thirty-one genera are recognized, six of which have been established heretofore by Miss Perkins. The species are 253 in number, by far the largest genera being Siparuna (89 spp.) and Mollinedia (71 spp.).—J. M. C.

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[2] Mem. Torr. Bot. Club **11**: 1–134. *pls. 1–19.* 1901.

[3] CHURCH, A. H.: On the relation of phyllotaxis to mechanical laws. Part I. Construction of orthogonal trajectories. pp. 38. *figs. 34.* Oxford: Williams and Norgate. 1901. 3s. 6d.

"EXCURSION FLORAS" are useful in Europe, but no one has as yet included the whole of Europe. Franz Thonner[4] has just made the attempt, but is able to include only the genera of flowering plants. Characters are used so far as possible which do not demand the microscope for determination, and the keys have been constructed with a view to rapid and easy use. Not only are the genera of Europe included, but also those of Iceland, the Azores, the Urals, and the Caucasus. The work follows the families and their sequence as given in Engler and Prantl's *Die natürlichen Pflanzenfamilien.*—J. M. C.

DR. AUGUSTIN GATTINGER[5] has published a list of the vascular plants of Tennessee. This veteran botanist has long been active in the study of the very interesting flora of his state, and this volume forms a permanent record of his results. It includes 2218 species and follows the Engler and Prantl sequence. The title "Philosophy of botany" covers general papers under the titles "An epitome of the history and philosophy of botany," "The forest," "The introduction of a national forestry policy in the United States," and "Modern thoughts on the origin, evolution, and significance of life." Applications for copies should be sent to the author at Nashville, and should enclose ten cents for postage.—J. M. C.

THE TWELFTH ANNUAL REPORT (1901) of the Missouri Botanical Garden contains the following scientific papers: A disease of the black locust (*Robinia Pseudacacia* L.) with 3 plates, by HERMANN VON SCHRENK, being an account of the attacks of *Polyporus rimosus* Berk.; Crotons of the United States, with 28 plates, by A. M. FERGUSON, containing descriptions of 33 species and varieties, 6 of them being new; An undescribed Agave (*A. Treleasii*) from Arizona, with 3 plates, by J. W. TOUMEY; A cristate Pellaea, with 1 plate, by WILLIAM TRELEASE; A Pacific slope palmetto, with 3 plates, by WILLIAM TRELEASE, being a new species of Sabal (*S. Uresana*); Garden beans cultivated as esculents, with 10 plates, by H. C. IRISH, being a synoptical description (75 pp.) of the numerous culture forms.—J. M. C.

THE PROCEEDINGS of the Indiana Academy of Sciences for 1900 has just been distributed, and contains the following papers of botanical interest: A presentation of the possibilities of photomicrography, with twenty-two half-tone illustrations, by D. W. DENNIS; Cryptogamic collections made during the year, and Experiments with smut, by M. B. THOMAS; Flora of Lake Maxinkuckee, by J. T. SCOVELL; Generic nomenclature of cedar apples, by J. C. ARTHUR; Additions to the flora of Indiana, and Some midsummer plants of southeastern Tennessee, by STANLEY COULTER; A bacterial disease of tomatoes, by WILLIAM STUART; Description of certain bacteria obtained from nodules of various leguminous plants, by SEVERANCE BURRAGE; Mycological notes from Wells and Whitley counties, by E. B. WILLIAMSON.— J. M. C.

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[4] Excursionsflora von Europa. Anleitung zum Bestimmen der Gattungen der Europäischen Blütenpflanzen. 12mo. pp. x+356. Berlin: R. Friedländer and Sohn. 1901. *M.* 4.

[5] The flora of Tennessee and a philosophy of botany. 8vo. pp. 296. Published by the authority of the state through the Bureau of Agriculture. 1901.

NOTES FOR STUDENTS.

JOST[6] has published an interesting and valuable summary of the recent contributions to our knowledge of the synthesis of proteids. Recent workers generally agree, in contrast with the older view of Schimper, that proteid synthesis can take place in the dark and in tissues without chlorophyll, provided carbohydrates are at hand.— H. C. COWLES.

F. E. WEISS,[7] after examining a very large number of specimens of Lepidophloios and Lepidodendron, has concluded that the arrangement of the cells making up the phloem region, at least as seen in transverse section, not only does not preclude them from being of the nature of true phloem elements, but makes it very probable that the function of this tissue was that of a normal phloem.—J. M. C.

BENJAMIN D. GILBERT[8] has published a useful list of North American pteridophytes. According to the editor, the four objects in view were (1) to present a convenient alphabetical list; (2) to make a list as comprehensive as possible in including all published forms; (3) to have a complete list which uses a conservative nomenclature; and (4) to publish the list of varieties of *Athyrium filix-foemina* which the author has found.—J. M. C.

J. W. HARSHBERGER[9] has been investigating the limits of variation in certain plants by the statistical method, largely as a contribution to the problem of species. Variations in size and shape of leaves, in weight and volume of fruit, and in number of seeds were tabulated. In *Liriodendron*, *Tulipifera*, *Sanguinaria Canadensis*, and *Ailanthus glandulosa* it was found that variation in size and form is due in part to the persistence of juvenile forms.— J. M. C.

THE GRASSES OF IOWA[10] is the title of a volume prepared by Professors

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[6] Biol. Cent. **20**: 625–637. 1900.

[7] On the phloem of Lepidophloios and Lepidodendron. Manchester Memoirs **45**: no. 7. *pls. 2–3.* 1901.

[8] Working list of North American pteridophytes (north of Mexico), together with descriptions of a number of varieties not heretofore published. Utica, N. Y.: Published for the Editor. 1901.

[9] The limits of variation in plants. Proc. Philad. Acad. **53**: 303–319. 1901.

[10] Iowa Geological Survey. Bulletin No. 1. pp. 525, with 220 illustrations. 1901.

L. H. Pammel and J. B. Weems of the Iowa State College of Agriculture, and F. Lamson-Scribner, agrostologist of the U. S. Department of Agriculture. The present volume is general and preliminary, bringing together a large amount of material in reference to the structure of grasses, the purity and vitality of grass seed, cereals, fungus diseases of grasses, bacterial diseases, pastures and meadows of Iowa, weeds of meadows and pastures, chemistry of foods and feeding, and lawns and lawn making in Iowa.—J. M. C.

ERWIN F. SMITH[11] has published the detailed results of his studies of some yellow forms of Pseudomonas. The investigation was very exhaustive, dealing with growth in fluid and solid media, sensitiveness to acids, diastasic action, aerobism, relative nutrient value of carbon compounds, temperature experiments, formation of acids and alkalies, reduction experiments, tests for hydrogen sulfid and nitrites, formation of indol, ferments, pigment studies, nature of the cell wall, vitality, and diagnostic characters. The four species studied, in the order mentioned in the title, are concerned with diseases of hyacinths, cabbages, beans, and sweet corn.—J. M. C.

FRIEDEL[12] claims to have observed the synthesis of carbohydrates, as measured by the absorption of carbon dioxid and emission of oxygen, without the presence of a living organism. Leaves were treated with glycerin under pressure and an extract obtained. A green powder was obtained from leaves heated to a temperature of over 100° C. Upon the exposure of a mixture of the leaf powder and extract to the light, oxygen was given off and carbon dioxid absorbed. Friedel concludes that synthesis is accomplished with or without the presence of living matter by means of a diastase which uses the energy of the solar rays. Chlorophyll is supposed to act as a sensitizer.—H. C. COWLES.

THE SECOND PART of the second volume of the "Catalogue of the African plants collected by Dr. Friedrich Welwitsch in 1853–61," and published by the British Museum, has just appeared. It contains the cryptogams, which have been distributed among investigators as follows: pteridophytes by W. CARRUTHERS; mosses by ANTONY GEPP, including 10 new species and a new genus (*Trachyphyllum*) near Erythrodontium; liverworts by F. STEPHANI, including 7 new species; marine algae by ETHEL S. BARTON; freshwater algae by W. WEST; diatoms by T. COMBER; lichens by E. A. WAINIO, 83 new species being described; fungi by ANNIE L. SMITH; and "Mycetozoa" by ARTHUR LISTER.—J. M. C.

[11] Compt. Rend. **132**: 1138–1140. 1901.

[12] The cultural characters of *Pseudomonas Hyacinthi, P. campestris, P. Phaseoli*, and *P. Stewarti*, four one-flagellate yellow bacteria parasitic on plants. Bulletin 28 U. S. Department of Agriculture, Division of Vegetable Physiology and Pathology. Pp. 153. August 6, 1901.

A NEW FASCICLE of Urban's *Symbolae Antillanae*[13] has appeared. It contains the conclusion of the monograph of Arthrostylidium by PILGER, 10 species being recognized, 4 of which are new; an enumeration of Gesneriaceae by Urban, including descriptions of 15 new species; a synopsis of Myrsinaceae by MEZ, with a recasting of several genera and descriptions of 11 new species; a synopsis of Theophrastaceae by MEZ, including two new species: descriptions of new species and genera by URBAN, the latter being *Hyptiodaphne* (Thymeleaceae), and three new genera of Compositae, namely, *Tetraperone*, *Koehnela*, and *Notoptera*, all of them Helianthoideae; and descriptions of 10 new liverworts by STEPHANI.—J. M. C.

BY USING an improved apparatus which enabled him to measure quickly and accurately small amounts of CO_2, Kolkwitz[14] has been able to determine that air dry grains of barley containing about 15 per cent. of water, which gradually diminished in the laboratory to 10 or 11 per cent., respired at a rate which produced in 24 hours one-third to one-half a milligram of CO_2 per kilogram of seeds. At 33 per cent. of moisture 2000 milligrams of CO_2 were produced. He also found both embryo and endosperm very tenacious of life. Respiration continued for several hours after such hard treatment as grinding. A full description of the apparatus with figures and an extended account of the investigation will be published in the organ of "Das Institut für Gährungsgewerbe und der Versuchsbrauerie in Berlin."—C. R. B.

TAMMES[15] has made an important investigation on the distribution of carotin. He agrees with most recent authors in identifying carotin with xanthophyll or chlorophyll-yellow and etiolin. Tammes goes somewhat further than most previous investigators in considering practically all red to yellow plastid pigments as carotin. Plastid pigments were examined and found to exhibit carotin tests in green and etiolated leaves, yellow parts of variegated leaves, autumn leaves, flowers, fruits, seeds, diatoms, algæ (green, blue-green, brown, and red), and carrot roots. Carotin always accompanies chlorophyll, appearing before it and remaining after it has gone, and also occurs where chlorophyll is always absent. Carotin is probably more or less efficient in carbohydrate synthesis, as Engelmann has shown. — H. C. COWLES.

HANS HALLIER[16] has presented a somewhat extensive regrouping of angiosperms, taking into account contributions from all departments of botany which may have given suggestions as to possible relationships. In other words, he has abandoned the customary morphological method and has called to his aid anatomy, embryology, physiology, "biology," and plant geography. He regards the Polycarpicae (Ranunculaceae, *et al.*) as the most primitive angiosperms, from which have come all other dicotyledons (especially Amentiferae and Sympetalae) on the one hand, and the monocotyledons on the other. He also thinks that the Convolvulaceae are not to be associated among the Tubiflorae, but are related to the Sapotaceae, Malvaceae, etc., and belong to the Ebenales which originated in the neighborhood of the Anonaceae. A great number of families and alliances are shifted in this way, the details being too numerous to be given in this notice, needing full presentation to be appreciated.—J. M. C.

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[13] Symbolae Antillanae seu fundamenta florae Indiae occidentalis. Vol. II. Fasc. 3. pp. 337–507. Leipzig: Gebrüder Borntraeger. 1901. *M* 9.90.

[14] Ber. deutsch. bot. Gesell. **19**: 285–287. 1901.

[15] Flora **87**: 205–247. 1900.

[16] Ueber die Verwandtschaftsverhältnisse der Tubifloren und Ebenalen, den polyphyletischen Ursprung der Sympetalen und Apetalen, und die Anordnung der Angiospermen überhaupt. Abhandl. Geb. Naturwiss. Verein Hamburg **16**: 1–112. 1901.

THE ADDRESS of Dr. B. L. Robinson as retiring president of the Botanical Society of America, entitled "Problems and possibilities of systematic botany," and delivered last August at the Denver meeting, has now been issued as a publication (no. 18) of the Society. The author's summary is as follows: "It may be said that systematic botany is very far from being a completed subject, that from our present standpoint we can see in various directions long vistas of further possibilities for fascinating explorations and profitable discovery, that among the subjects which seem to invite immediate attention the most important are: (1) The determination of the modes and degrees of variation, an investigation which alone can yield data for a more critical discrimination of plant categories; (2) far more complete study of plant ranges, which can scarcely fail to throw much new light upon the forces controlling distribution; and (3) a further examination of plant ontogeny as the most hopeful source of information regarding the more intimate affinities and proper arrangement of plants."—J. M. C.

GIESENHAGEN[17] reports some observations made by him in 1891–2 upon the growth of the rhizoids of Chara, which seem to confirm the recent theories and observations of Haberlandt, Noll, and Němec, on the perceptive organs for geotropic stimuli. When young rhizoids of Chara were directed upward there was first a retardation of their growth, with subsequent recovery of the previous rate, and soon a curvature which directed the tip of the rhizoid again downward. Similar retardation followed the placing of the young rhizoid in a horizontal position and a downward curvature also occurred. Near the tip of the rhizoid Giesenhagen found a group of small granules which altered their position when the rhizoids were displaced. The change in the position of these relative to the sensitive cytoplasm, he regards as producing the immediate stimulation from which curvature results. The nature of these minute granules has not been ascertained, but in this terminal cell of the rhizoid they seem to play the same rôle as (according to Němec) the starch grains do in the cells of the root tip.—C. R. B.

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[17] Ber. deutsch. bot. Gesell. **19**: 277–285. *pl. 12.* 1901.

STRASBURGER [18] has recently investigated the formation of pollen in *Asclepias Cornuti* and *Cynanchum vincetoxicum*, having in view chiefly the reported lack of tetrad formation in some of the Asclepiadaceae. A primary sporogenous cell develops directly into a spore mother cell, as in Malva, Datura, Mentha, and Chrysanthemum, being recognized by the reduction in the number of chromosomes. Each mother cell gives rise to four pollen grains as in other plants, but instead of lying in the usual tetrad form they develop in a row. This leaves the Cyperaceae as the only group known to form only one pollen grain from each mother cell. The row of four microspores is homologized with the row of four potential megaspores commonly produced by the primary sporogenous cell in the nucellus. The regularity in the arrangement of the cells and the homogeneity of the protoplasm invited a search for centrosomes, but none were found. The author, while not denying the existence of centrosomes in the higher plants, expresses an increasing doubt as to the possibility of making such structures visible with the present methods.—T. C. FRYE.

FREDERICK H. BILLINGS [19] has examined a number of species of several large families of spermatophytes to see whether the seed development, especially the changes of the embryo sac and integuments after fertilization, can be used as a basis of classification. Taking plant groups as now recognized, in some he finds marked resemblances. For example, in all species of Campanulaceae, Lobeliaceae, and Stylidaceae he finds "haustoria" (outgrowths from the embryo sac) at both chalazal and micropylar ends, and these are supplied with nuclei from the endosperm. The antipodal ones break down, but may divide first; while in Calendula the micropylar haustorium is said to be under the control of the persistent synergid, which grows into it. The various kinds of haustoria are described in detail. In some cases the embryo sac is constricted, the upper chamber containing the embryo, the lower becoming filled with tissue. In other cases finger-like processes put out from the side or base of the sac, reaching towards the region of vascular bundles. The author's reason for assigning a nutritive function to the "haustorium" regions is simply the active appearance and staining power of the nuclei. His conclusions are that in doubtful cases the nature of the embryo sac, the thickness of the integument, etc., may help to settle the systematic position of a genus or species.— FLORENCE MAY LYON.

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[18] Einige Bemerkungen zu der Pollenbildung bei Asclepias. Ber. deutsch. bot. Gesell. **19**: 450–461. *pl. 24.* 1901.

[19] Beiträge zur Kenntniss der Samenentwickelung. Flora **88**: 253–318. 1901.

A paper on *Tulipa Gesneriana* by Alfred Ernst[20] adds another species to the list of seed plants showing polyembryony, and also confirms Guignard's observation of double fertilization in this species. The author has followed out the development of the embryo sac in a close series, discovering no marked variation from the usual method. In fertilization the second male nucleus unites with the upper polar nucleus and both unite with the lower polar, the three remaining distinct and showing no evidence of fusion. The interest of the paper, however, centers about the development of the embryo. The fertilized egg divides by a longitudinal or transverse wall, and sometimes by an oblique wall. From these cells there develops by means of irregular cell division a compact mass of large cells rich in protoplasm and containing many nuclei. This "proembryo" forms at its apex from one to six embryos, only one of which as a rule develops into a normal embryo. The other embryos, as well as the cells of the "proembryo," are resorbed and devoted to the building up of the embryo proper. This is a case of polyembryony similar to that discovered by Jeffrey and also by Hofmeister in Erythronium. The author endeavors to follow out the reduction and doubling of the chromosomes, but this part of the paper is far from satisfactory. A valuable résumé of the literature of polyembryony is included in the discussion. The figures are carefully drawn and adequate to explain the points considered.—J. B. Overton.

Items of taxonomic interest are as follows: C. R. Ball (Proc. Iowa Acad. Sci. **7**: 141–154. 1900) has published an account of the 14 species of Salix occurring in Iowa.—E. S. Steele (Proc. Biol. Soc. Washington **14**: 47–86. 1901) has published the 6th list of additions to the flora of Washington, D. C., and vicinity, with descriptions of new species of Viola and Lycopus.—F. N. Williams (Jour. Bot. **39**: 289–294, *pl. 425*. 1901) has separated Salisbury's genus Ianthe from Hypoxis.—F. V. Coville (Proc. Wash. Acad. Sci. **3**: 297–362. *pls. 33–42*. 1901) has published a very full and handsomely illustrated account of the willows of Alaska, including 23 species, one of which is new.—Elias Nelson (Proc. U. S. Nat. Mus. **23**: 697–713. 1901) has published a revision of 35 species of Antennaria, 4 of them being new.—K. Fr. Meinshausen (Acta Hort. Petrop. **18**: 9–415. 1901) has published a synopsis of the Cyperaceae of European and Asiatic Russia. New species are described under Kyllingia (1), Cyperus (3), Scirpus (5, including Eleocharis), Eriophorum (2), Schoenus (1), Kobresia (2), and Carex (25), the last genus being represented by 215 species.—V. L. Komarov (*idem* 419–449) has described numerous new species from Manchuria and northern Korea, among them a new genus (*Boehmeriopsis*) of Urticaceae and 9 new species of Carex.—O. F. Cook (Bull. Torr. Bot. Club **28**: 525–569. *pls. 43–48*. 1901) has published a synopsis of the palms of Porto Rico, including 20 species, representing 14 genera and 4 families. The startling fact is that 7 of the genera and 13 of the species are new. *Inodes*, *Thrincoma*, and *Thringis* are new genera of Sabalaceae; *Aeria* and *Acrista* of Arecaceae; *Curima* and *Cocops* of Cocaceae. The plates are of unusual beauty.—E. P. BICKNELL (*idem* 570–592), in his ninth paper entitled "Studies in Sisyrinchium," presents the species of Texas and the southwest, the number reaching 25, of which 17 are new.—J. M. C.

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[20] Beiträge zur Kenntniss der Entwickelung des Embryosackes und des Embryo (Polyembryonie) von *Tulipa Gesneriana*. Flora **88**: 37–77. *pls. 4–8*. 1901.

NABOKICH in a preliminary communication to the German Botanical Society[21] claims to have demonstrated that the growth of the higher plants may take place under conditions which prevent normal respiration, and that the reason why previous investigators have found no anaerobic growth is that their experiments were carried on under conditions which permitted the wilting of the experimental material. His method consists in putting into a $50-70^{cc}$ flask with tubulated neck, $40-50^{cc}$ of a 0.5 to 2 per cent. solution of glucose or cane sugar. Into this nutritive solution he puts etiolated seedlings of maize, sunflower, onion, etc., or cuttings of vigorous stems and roots which have been kept previously in water for one to four hours. The parts are marked with fine lines to serve as data for growth. After putting these into the flask, the top of the neck is fused off, and after cooling the air is exhausted *via* the side tube, which is previously drawn down at one point to a thick capillary. After exhaustion to a minimum the flask is partly sunk in hot water. The nutritive solution boils violently and the escaping vapor aided by the continued exhaustion with the air pump removes the last trace of oxygen. Five to eight minutes suffice to remove the oxygen and the side tube is then fused off. The whole operation should be complete in a half to three quarters of an hour. Seedlings of maize showed 7.5^{mm} growth in 36 hours, cuttings from the stem of maize 8.2^{mm}, and cuttings of stem of sunflower 5^{mm} in 45 hours. In various seedlings curvatures developed which are precisely similar to those which are formed in the air under similar stimuli. No formation of chlorophyll was observed.

These results stand in sharp contradiction to those of most observers, whose source of error Nabokich undertakes to specify. In a later number of the same periodical Wieler replies to Nabokich's strictures and maintains the accuracy of his own results. The question evidently needs further investigation.—C. R. B.

MISS MARGARET C. FERGUSON[22] has published the results of her studies in Pinus. A detailed account of spermatogenesis in five species is given,

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[21] Ber. deutcsh. bot. Gessell. **19**: 222–236. 1901.

[22] The development of the pollen tube and the division of the generative nucleus in certain species of pines. Ann. Bot. **15**: 193–223. *pls. 12–14.* 1901.

The development of the egg and fertilization in *Pinus Strobus*. *Ibid.* 435–479. *pls. 23–25.*

and of oogenesis, the phenomena of fertilization, and the early segmentations in *P. Strobus*. In the main, there is abundant confirmation of the more fragmentary work of previous investigators. Besides, the genus has been found variable enough to make the full study of any species valuable. Some of the points to be noted are as follows: The "antheridial" (generative) cell is said to divide "before the beginning of winter," which indicates a wide range of time in the genus for this event. A definite order of precedence for the stalk and "generative" (body) cells in the pollen tube is given, the former being said to pass the latter and consort with the "vegetative" (tube) nucleus. The body cell is said to be peculiar in never being limited by a cell wall, and a survival of the centrosome is suggested in the division of its nucleus. The interesting claim is made that "sperm cells are never formed, but the sperm nuclei remain surrounded by a common mass of cytoplasm," and become unequal very early in their history. In some cases, after fertilization, the tube and smaller sperm nuclei were observed to divide amitotically. The most interesting fact in connection with fertilization and segmentation is that in addition to the well-known fact that there is no real fusion of the sexual nuclei in fertilization, the author has been able to observe that "the two chromatic groups remain distinct until the nuclear plate stage" of the first segmentation. No centrosomes are claimed for the first segmentation, "but the entire activity connected with this mitosis indicates that the sperm nucleus, under the influence of the egg cytoplasm, is the agent which initiates and controls the division." The frequently noted similarity between the fertilization processes in the gymnosperms and animals is presented in considerable detail. These papers are valuable additions to our rapidly increasing literature of gymnosperms.—J. M. C.

OPEN LETTERS.

NORMAL SOLUTIONS.

RECENTLY Mr. James B. Dandeno published an article[1] in which he accuses Kahlenberg and True[2] of having confused solutions containing gram-equivalents per liter with such as contain gram-molecules per liter. Because of the prominence given to Mr. Dandeno's article by publication in the BOTANICAL GAZETTE, I feel compelled to write this reply.

Kahlenberg and True have used both expressions, gram-equivalent per liter and gram-molecule per liter, but they have not confused them. In the case of mono-basic acids and salts of mono-basic acids with monad metals a solution containing a gram-equivalent per liter is identical with a solution containing a gram-molecule per liter, and hence in such cases the terms are perfectly interchangeable. This fact Mr. Dandeno evidently overlooked and so he saw great confusion where none existed.

It will be necessary to take up Mr. Dandeno's points somewhat in detail. The expression, "Chemically equivalent quantities (*i. e.* molecular quantities) of the different substances were not compared," which Kahlenberg and True used on p. 85 of their article, occurs in the course of the general introduction and does not warrant (especially when taken together with the further discussion in the article) the conclusion of Mr. Dandeno that "they regard a gram-molecule per liter exactly the same as a gram-equivalent per liter." On p. 91 Kahlenberg and True say, referring to the various tables that follow, "In the first column appear the concentrations used expressed in gram-molecules or gram-equivalents per liter of the solution." As both expressions actually appear, and are properly used, in the headings of the tables that follow, the above statement (which refers to all the tables in the article, except tables 18 and 19 concerning which special mention is made on p. 97) *in itself* clearly does not warrant Mr. Dandeno's conclusion that the authors regarded a gram-molecule per liter as exactly the same as a gram-equivalent per liter.

Mr. Dandeno states that the normal solution of sulfuric acid used by Kahlenberg and True was "purchased from the chemist" and that it was "a gram-equivalent solution and was thought to be a gram-molecule solution." No statement is made by Kahlenberg and True that any solution was "purchased from the chemist," and Mr. Dandeno's inference is wholly baseless.

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[1] BOT. GAZ. **32**: 229, Oct. 1901.

[2] BOT. GAZ. **22**: 124, Aug. 1896.

As a matter of fact, I happen to be the chemist who prepared the normal sulfuric acid solution as well as the other solutions used by Dr. True and myself, and the strengths of all the solutions were exactly as indicated in the columns of the tables. The results of Kahlenberg and True indicate that $\frac{1}{6400}$ gram-equivalents of H_2SO_4 per liter is as toxic as $\frac{1}{6400}$ gram-equivalent of HCl per liter, and not that $\frac{1}{6400}$ gram-equivalent of H_2SO_4 per liter is as toxic as $\frac{1}{3200}$ gram-equivalent of HCl per liter as Mr. Dandeno states; this shows how much care he used in scrutinizing the tables he attempts to criticise.

Kahlenberg and True have found that a solution containing $\frac{1}{6400}$ of a gram-equivalent of H_2SO_4 (*i. e.* $\frac{49}{6400}$ grams) per liter is as toxic as a solution containing $\frac{1}{6400}$ of a gram-equivalent of $KHSO_4$ (*i. e.* $\frac{136}{6400}$ grams) per liter. Since $KHSO_4$ contains but one hydrogen atom, which is the active agent under consideration, either the term gram-equivalent or gram-molecule might be used concerning this substance, for they mean the same thing here; as a matter of fact the term gram-equivalent is used in Kahlenberg and True's table. There is no confusion in Kahlenberg and True's article on this point, as Mr. Dandeno thinks. On the bottom of p. 91 of Kahlenberg and True's paper is the statement, "Tables 1 to 5 show that the seedlings just survive in a solution that contains $\frac{1}{6400}$ gram of hydrogen ions per liter," which might have shown Mr. Dandeno that no confusion exists, had he read it with sufficient care.

To be sure Ostwald in his tables of electrical conductivity expresses the concentrations of the solutions in gram-molecules per liter; but this does not prevent one from calculating from these tables the degree of dissociation of a salt in a solution, the strength of which is expressed in gram-equivalents per liter, as Mr. Dandeno seems to think. Kahlenberg and True were well aware of the true character of Ostwald's tables, and in referring to them, and in calculating the dissociation from them, they took into consideration the fact that the tables are based on gram-molecules per liter. Take the case of maleic and fumaric acids of which Mr. Dandeno makes a special point. These acids are both dibasic. In Ostwald's tables[3] we find that when 1 gram-molecule of maleic acid is contained in 2048 liters, the degree of dissociation is 98.2 per cent.; and when 1 gram-molecule of fumaric acid is contained in 2048 liters the degree of dissociation is 78.5 per cent. Now in the case of a dibasic acid, a solution containing 1 gram-molecule in 2048 liters is clearly identical with a solution containing 1 gram-equivalent in 1024 liters; and so when Kahlenberg and True state "as maleic acid at the dilution 1024 is dissociated 98.2 per cent. and fumaric acid 78.5 per cent. we should expect the latter to be less poisonous than the former if the toxic action be due to H ions alone," they are perfectly correct. Moreover the tables (58 and 59, p. 115 of

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[3] Zeitschrift physik. Chem. **3**: 380.

Kahlenberg and True) concerning these acids are both clearly headed "gm. equiv. per liter," which excludes all possibility of misconception. Mr. Dandeno clearly is in error; and for the piquant remarks in which he indulges on p. 234 of his article in referring to the comments of Kahlenberg and True on the behavior of maleic and fumaric acids, he deserves sharp censure.

Mr. Dandeno further complains that Heald[4] states in referring to Kahlenberg and True, "in these experiments the solutions were prepared according to gram-equivalents," and then Dandeno adds that on pp. 119–123 of Kahlenberg and True we find written "gram-mol. per liter." Now it happens that all the acids listed on pp. 119–123 by Kahlenberg and True are mono-basic acids, and that in the case of these a gram-molecule per liter is identical with a gram-equivalent per liter, so that Heald was correct in his statement. Evidently Mr. Dandeno failed to note the basicity of the acids listed by Kahlenberg and True on the pages last mentioned.

The two instances that Dandeno mentions, in which Kahlenberg and True have stated that a gram-equivalent is contained in so many liters of water instead of so many liters of solution, are cases in which the solutions in question were so extremely dilute, that no difference could be detected were the solutions made up on the one basis or the other. The instances occur, moreover, in the course of a preliminary general discussion where no sharp comparison is involved.

I have not taken the time to look up the work of the various other investigators that Mr. Dandeno attempts to criticise. It is of course possible that mistakes have been made; but from what has been said above, the reader can readily form an opinion as to Mr. Dandeno's competency to make such criticisms.

In conclusion, I wish to emphasize once more that all the solutions used by Kahlenberg and True were of exactly the strengths indicated in their tables, that the conclusions based upon them are correct, and that the interpretations of Mr. Dandeno are entirely wrong.— LOUIS KAHLENBERG, *Laboratory of Physical Chemistry, University of Wisconsin.*

I am limited to a brief reply to the foregoing letter. Regarding it I have to say:

It is fully explained in my paper[5] that, in the case of monobasic acids and salts with monad metals, gram-molecule and gram-equivalent solutions are the same. It was only where basicity differed that exception was taken.

In view of Dr. Kahlenberg's assertion, I withdraw fully the statement that the solution of sulfuric acid referred to was purchased from the chemist. I had Dr. True's statement that it was, but I must have misunderstood him.

However, Dr. True states,[6] referring to this table (H_2SO_4) headed

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[4] BOT. GAZ. **22**: 125. Aug. 1896.

[5] BOT. GAZ. **32**: 230–232. Oct. 1901.

[6] Quoted *l. c.*, p. 233.

"gram-equival. per l.," that, in chemical equivalent quantities of H_2SO_4 and of HCl, there are twice as many H ions in the H_2SO_4 as there are in the HCl. Dr. True clearly regarded this as a gram-molecule per liter solution, so my reference to this point is not without good ground.

Since Heald referred to the whole paper of Kahlenberg and True, and since several dibasic salts are there[7] listed "gram-molecule per liter," my general reference is abundantly warranted.

An illustration will make clear one misconception. Dr. Kahlenberg states that gram-molecule and gram-equivalent solutions of $KHSO_4$ are the same. I hold they are not. In a gram-equivalent per liter solution of $KHSO_4$ there is *one-half* gram of H. Dr. Kahlenberg's position is that there is *one* gram of H. If I misinterpret this substance I am in good company. (See definition gram-equivalent and references to Talbot, Mohr, Sutton, Fresenius, p. 230.)

As to dissolving substances in so much *water* or in so much *solution*, I may say that I am surprised at Dr. Kahlenberg's defending, *in any case*, the former method.

My paper was not written as a criticism of Kahlenberg and True, as he seems to think, though their work was freely drawn upon for illustration.—JAMES B. DANDENO, *Normal and High School, St. Louis, Mo.*

BASILIMA, SCHIZONOTUS, SORBARIA.

IN THE July number of the BOTANICAL GAZETTE (**32**: 56) Mr. Alfred Rehder discusses these names, reaching the conclusion that Sorbaria is the proper designation for the genus in which *Spiraea sorbifolia* Linn. is now placed. His decision in the case of *Basilima* Raf. seems unquestionable, viz., that when it first appeared, in 1815, it was a *nomen nudum*, and when republished in 1836 it was a synonym of *Schizonotus* Lindl. But why *Schizonotus* Lindl. should be set aside is not so clear to me. It is said that where it was first published, in Wallich's *Catalogue* (no. 703; Pritzel says that this portion of the *Catalogue* appeared 1 D 1828), this name was a synonym. The *Catalogue* is cited fully and correctly: "no. 703, Spiraea Lindleyana Wall. Schizonotus Lindl. (gen. nov. Spir. sorbifoliam amplectans)," but I fail to see how there is any synonymy here; if so, of what is Schizonotus a synonym? We have here rather an annotation. Wallich's *Spiraea Lindleyana* is said to belong to the new genus *Schizonotus* Lindl., based upon *Spiraea sorbifolia*. *Spiraea Lindleyana*, like most of the other names of Wallich's *Catalogue*, when divorced from the specimens which were intended to accompany it, is merely a *nomen nudum*; while *Schizonotus*, distinctly based upon a well-known species, *Spiraea sorbifolia*, is certainly not a *nomen nudum*, and can scarcely be held a synonym of one!

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[7] BOT. GAZ. **22**: 96. ($CuSO_4$, etc.)

Again, it is claimed that the second publication of *Schizonotus* (Lindl. *Introd. Nat. Syst.* 81. 1830) is as a synonym. Again Mr. Rehder quotes correctly, but, as it appears to me, draws wrong conclusions. Lindley says: "*Spiraea sorbifolia* (Schizonotus m.)." This is not synonymy, but annotation. Of course, "Schizonotus m." is an abbreviation of "Schizonotus mihi," and the case is precisely the same as if Lindley had written in full: "*Spiraea sorbifolia* (which I have distinguished as a separate genus under the name *Schizonotus*)." Surely this is not synonymy. If so, why does Lindley, two pages farther on, in naming the typical genera of Spiraeaceae, enumerate "Spiraea, Gillenia, Schizonotus"?

Mr. Rehder admits that "in 1836, Lindley enumerates (p. 145) Schizonotus as a genus, and characterizes it (p. 441) by mentioning *Spiraea sorbifolia* as the type." What Lindley actually says (*Introd. Nat. Syst.* ed. 2, 441) is this: "Schizonotus, *Lindl. in Wall. Cat.*—Spiraea sorbifolia, etc." Am I pardonable if I fail to see why the name is published any more satisfactorily here than in either of the two preceding cases? And as far as the enumeration of Schizonotus as a genus on page 145 is concerned, I have already called attention to the fact that it was enumerated in the same way on page 83 of the first edition (1830).

Of course, *Basilima* Raf. 1815 being a *nomen nudum*, Seringe's sectional name *Sorbaria* was the first under which this group of plants was distinguished, but it was not used in a generic sense until 1864. It is true that the replacing of properly published generic names by earlier sectional ones has been suggested, but I am not aware that it has found any powerful advocate, even among extremists in nomenclatural reform, and I know of no botanist who has consistently carried out this principle. Yet such a principle seems to be the only excuse for the use of the name *Sorbaria*. Botanists who accept the oldest generic name must take up *Schizonotus* Lindl. 1828, while those (few of them in America, I believe) who adopt the generic name with which a specific name is first combined must use *Basilima* Raf. 1836, if they are to be consistent with their principles. It is scarcely necessary to refer to Mr. Rehder's remark that "it would be very unfortunate to revive the name Schizonotus, since it was applied afterwards and has been in use for two other genera," as this is an argument which will carry little weight with most people, and one which I believe Mr. Rehder himself would hardly have advanced as the only reason for discarding *Schizonotus*.

"Sorbaria of course will not enter into the American flora if Chamaebatiaria is considered as constituting a distinct genus" is another statement to which I must take exception. On the contrary, *Schizonotus sorbifolius* (L.) Lindl. (Steud. *Nomencl.* 531. 1841), the type of the genus, is peculiarly adapted to the conditions prevailing in the northeastern United States, and is winning its right to a place in our manuals as an introduced plant. It was reported from central New York ten years ago (Peck, Rep. N. Y. State Mus. **44**: [15]. 1891), and I found it myself in the northern part of this county (Westchester Co., N. Y.) in July 1895. It was at that time that I became interested in the synonymy of this genus, and Mr. Rehder's article brought vividly to mind the researches which I then conducted upon this subject.

Since writing the above I notice that the plant under discussion has been admitted to Dr. Britton's recently published *Manual*.—JOHN HENDLEY BARNHART, *Tarrytown, New York.*

NEWS.

Dr. W. R. Shaw has been appointed botanist of the Oklahoma Experiment Station.

At the University of Wisconsin, Charles E. Allen has been appointed instructor in botany, and Mrs. George J. Ruger and H. A. Winkenwerder assistants in botany.

Houghton, Mifflin and Company announce that Sargent's *Silva of North America* is to be supplemented by two additional volumes, containing 115 plates. The volumes will be published in 1902.

A biographical sketch of Dr. Charles Mohr, prepared by Eugene A. Smith, and accompanied by an excellent portrait, is published in the November number of the *Bulletin of the Torrey Botanical Club.*

In the November number of the *Journal of the N. Y. Botanical Garden* the report of Dr. N. L. Britton on his recent trip to the West Indies is published, and also the report of Professor L. M. Underwood on a trip to Porto Rico.

An excellent portrait of M. Maxime Cornu is published in *Bull. Soc. Bot. de France* of September last, in connection with an account of his obsequies. The address at the tomb was given in behalf of the society by M. Ed. Bureau.

Herman B. Dorner has been appointed assistant in botany in the Indiana Agricultural Experiment Station at Purdue University, *vice* Wm. Stuart, who has been transferred to the staff of the Horticultural department of the same station.

Dr. Hans Solereder, of Munich, has been appointed professor of botany and director of the Botanical Institute at the University at Erlangen. Dr. V. Schiffner, associate professor of systematic botany in the German University at Prague, has been called to a similar position in the University of Munich.—*Science.*

R. H. Denniston and H. G. Timberlake spent about two weeks in September collecting for the State University in the lake region of Vilas county, Wisconsin. Special attention was given to the lower cryptogams, of which about 450 species were collected. These included about 350 fungi and lichens, 50 algae, and 50 mosses.

Dr. Thomas Meehan, the well-known horticulturist and botanist, died at his home in Germantown, Philadelphia, on November 19, at the age of seventy-five. He was botanist of the State Board of Agriculture of Pennsylvania, in charge of the herbarium of the Philadelphia Academy of Sciences, and editor of *Meehan's Monthly*.

STEPHEN C. STUNTZ and Charles E. Allen, of the University of Wisconsin, spent the month of August and the early part of September in making collections and ecological notes of the flora of Isle Royale, Lake Superior. They worked chiefly about Rock Harbor, on the south shore of the island. Their collections include 480 numbers of spermatophytes, about 90 of pteridophytes, 340 of mosses and liverworts, 80 of lichens, and 650 of fungi and myxomycetes.

Bulletin du Jardin Impérial Botanique de St.-Petersbourg is the French form of the title of a new Russian botanical journal, three numbers of which have appeared, under the editorship of A. Fischer de Waldheim. It is to publish original papers, critical reviews, and reports from the Garden. At the end of each paper a brief résumé in French or German is given. Prominent among the contributors to the first three numbers are A. Elenkin, the lichenologist, and A. Jaczewski, the mycologist.

A GENERAL MEETING of botanists will be held at the University of Chicago on December 31, 1901, and January 1, 1902, in connection with the meeting of the American Society of Naturalists and affiliated societies. The local committee of arrangements extends an invitation to all botanists, whether members of any society or not, to attend the meetings (availing themselves of the *guaranteed* railroad rate of a fare and one-third on the certificate plan), to attend the reception and the annual dinner and to share in all provision made for the convenience and pleasure of visiting naturalists. Detailed announcements will be sent on request.

NEARLY TEN years ago the late Professor Thomas A. Williams and Mr. David Griffiths, now of Takoma Park, D. C., agreed to issue sets of fungi of South Dakota. Later this plan was changed to include the west in general. The death of Professor Williams caused an abandonment of the undertaking entirely until a recent invoice showed that an unusual amount of very valuable material had been accumulated. It is estimated that there are on hand about three centuries of specimens, containing many species recently described from South Dakota, Wyoming, Montana, and Arizona. The collection is rich in species of fungi that have never been distributed in any set of *exsiccati*. Mr. Griffiths, therefore, has determined to put the specimens up in packets with printed labels bearing the usual data, and to offer them for sale under the title *West American Fungi*. The original plan contemplated issuing fifty-four sets, but a much smaller number will now be put up. One century or three may be ordered, to be paid for when issued. The first century will be ready about the middle of December.

GENERAL INDEX.

The most important classified entries will be found under Contributors, Personals, and Reviews. New names and names of new genera, species, and varieties, are printed in **bold-face type**; synonyms in *italics*.

A

A. A. A. S., Denver meeting 75
Abies, needles of 356
Abnormalities 343
Acacia, amentacea 203, formation 272; Berlandieri 272, formation 273; Farnesiana 103, 111, formation 272; Wrightii formation 273
Acanthaceae, Lindau on 71
Acer grandidentata 263
Acerates, longifolia 326, viridiflora 326
Achlya 161
Acrista, Cook on 435
Actinella linearifolia 210
Aecidium Euphorbiae 421
Aeria, Cook on 435
Aestivation, abnormal 352
Agave, heteracantha formation 283; Toumey on 71, 428; vegetation 281
Agriculture, organization of Bureau of Plant Industry of the U. S., Department of 155
Alae, abnormal 351
Alaria, Saunders on new species of 374
Albugo, candida 91; gametogenesis and fertilization in 77, 157, 238; Portulacae 79; Tragopogonis 85
Alcoceria, Fernald on 153
Algae 309; of St. Paul city water, Fanning on 374; polymorphism in 292; Schmidle on 70; Setchell on 70; West on African freshwater 430
Allen, Charles E. 1; personal 443, 444
Allium Cepa, karyokinesis of 423
Alniphyllum, Matsumura on 377
Amarantaceae, Lopriore on 71
Amblyolepis setigera 210
Ambrosia artemisiaefolia 78
America, Urban on new plants of 71
Anderson, Alexander P., personal 154, 379
Andropogon furcatus 205
Anemone Caroliniana 106
Angiosperms, Hallier on classification of 431
Annuals, formation of prairie 201, 208
Antennaria, Nelson on 434
Apospory, in Anthoceros, Lang on 376
Apples in cold storage, Corbett on 151
Aquilegia, pollination in 304
Arceuthobium pusillum, Wheeler on 64
Archegonia of Selaginella apus 130
Argyrostachys, Lopriore on 71, 378
Aristida fasciculata formation 201
Arnica, Greene on 153
Arnold's "The sea beach at ebb tide" 222
Arnoldi, work of 173, 223
Artemisia frigida 263
Arthrostylidium, Pilger on 431
Arthur, J. C. 307; personal 74, 228; work of 374
Asclepiadaceae, pollen of 327
Asclepias, Cornuti 326, Strasburger on pollen in 433; decumbens 198; incarnata 326; phytolaccoides 326; speciosa 326; Syriaca 326; tuberosa 326; verticillata 326
Ashe, W. W., work of 68
Asplenium, Gilbert on 377
Auld and Gibson's "Codium" 63
Autran, Eugène, personal 227

B

Bacteria of leguminous plants, Burrage on 429
Bacterial disease of tomato, Stuart on 429
Baldwinia, Harper on 378
Balfour, Bayley, personal 380
Ball, C. R., personal 156; work of 434
Banker, H. J., work of 153
Barnes, C. R., 151, 369, 373, 375, 431, 432, 435
Barnhart, John H. 440
Barton, Ethel S., work of 430
Basilima 440
Basilima 56
Bast fibers, middle lamella of 18
Beal, W. J., personal 228; work of 153
Beattie and Piper's "Flora of the Palouse region" 62
Bees and flowers 367
Belajeff, work of 175, 177
Bennett, Arthur, 58

Bergen, J. Y., personal 307
Bernard, C. H., work of 70, 152
Bessey, C. E., personal 74, 228; "Structure and classification of diatoms" 150
Bessey, E. A., 64, 66, 67, 151; personal 156
Bicknell, E. P., work of 70, 377, 435
Billings, F. H., work of 433
Boehmeriopsis, Komarov on 434
Bogue, E. E., work of 68
Bolley, H. L., work of 68
Bosqueiopsis, Wildeman and Durand on 377
Botanical Society of America 380
Botany, Iowa Summer School of 76
Botrychium ternatum Oneidense, Gilbert on 71
Bower, F. O., personal 227; work of 178
Brackett, Gustavus B., personal 155
Bray, W. L., 99, 195, 262
Bravodendron, Small on 378
Britton, E. G., personal 228
Britton, N. L., personal 75; work of 71, 72, 153, 379, 443; "Manual of the flora of the northern states and Canada" 426
Brodie, D. A., work of 68
Bromeliaceae, Mez on 71
Bruchmann, work of 170
Bryobrittonia, Williams on 72
Bryonia dioica 368
Bulbilis dactyloides 119
Bulletin Jard. Imp. Bot., St. Petersbourg 444
Bumelia lycioides 268
Bunch grass 285
Bureau, Ed., personal 443
Burrage, Severance, work of 429
Butler, Eloise, personal 155
Butten, F. K., work of 374

C

Cactaceae, structural studies on 35
Cactus vegetation 278
Calcium oxalate, function of 142
Calyx, abnormal 351
Campanula rotundifolia 263
Campbell, D. H., personal 228; work of 174
Carbohydrates, Friedel on synthesis of 430
Cardiocarpon anomalum, sporangium of 180
Carex, Komarov on 434
Caricaceae, Urban on 71
Carlton, Mark Alfred, personal 156
Carotin, Tammes on distribution of 431
Carruthers, W., work of 430
Castilleia, Rydberg on 378
Celery blight, Townsend on 64
Cell plate, theory of 3
Cell wall 1
Cellulose 4
Cenchrus myosuroides 205
Central America, Fernald on plants of 153; Robinson on plants of 153
Centrosomes, in Helosis and Lilium, Bernard on 152; Yamanouchi on 375
Ceram, a tropical forest in 218
Ceramothamnion, Richards on 71
Cerastium, Green on 377
Cercospora apii, Townsend on 64
Cercosporidium, Earle on 377
Cercocarpus parvifolius 263
Cereus, caespitosus 280; Fendleri, anatomy of 40, vascular system of 37; giganteus, anatomy of 46, hypoderma of 38
Chaetonella, Schmidle on 378
Chamaebatiaria 58
Chamaelirium, Small on 377
Chamberlain, C. J. 64, 66, 67, 69, 150, 153, 223, 224; personal 156; "Methods in plant histology" 372
Chaparral 197, 274, 277; black 203; formation 206, 270, 276
Chesnut, V. K., personal 156
Chester, F. D., work of 151; "Manual of bacteriology" 370
Chlamydomonas, Whipple on 150
Chodat, R., work of 70, 71
Chondrogloea, Schmidle on 378
Christ, H., work of 153
Church's "Phyllotaxis" 427
Cicuta vagans, Brodie on 68
Clark, Anna M., work of 68
Classification by seeds, Billings on 433
Cleistogamous flowers, Du Sablon on 67
Clematis, abnormal flowers of 352
Clements, F. E., personal 75, 228; "Phytogeography of Nebraska" 374
Clinton, G. P., personal 154; work of 71
Clothier, G. L., work of 67
Coccomyxa, Schmidle on 71
Cockerell, T. D. A. 60
Cocops, Cook on 435
Coenocentrum 93, 244
Collenchyma, middle lamella of 20
Collins, Guy N., personal 154
Color, distribution of red 332
Comber, T., work of 430
Compositae, Rydberg on 378
Conidia, homology of 168
Convolvulus arvensis, Pammel on 68
Contributors: Allen, Charles E. 1; Arthur J. C. 307; Barnes, C. R. 151, 369, 373, 375, 431, 432, 435; Barnhart, John H. 440; Bennett, Arthur 58; Bessey, E. A. 64, 66, 67, 151; Bray, W. L.

99, 195, 262; Chamberlain, C. J. 64, 66, 67, 69, 150, 153, 223, 224; Cockerell, T. D. A. 60; Copeland, E. B. 356; Coulter, J. M. 62, 70, 153, 371, 373, 374, 375, 377, 426, 427, 428, 429, 430, 431, 432, 434, 435; Cowles, H. C. 374, 376, 429, 430, 431; Dandeno, J. B. 229, 439; Davis, B. M. 61, 63, 64, 222; Fairchild, David G. 218; Faull, J. H. 381; Fernald, M. L. 359; Frye, T. C. 325, 433; Hefferan, Mary 370; Holway, E. W. D. 421, 422; Johnson, T. C. 303; Kahlenberg, Louis 437; Kraemer, Henry 423; Land, W. J. G. 69; Lawson, A. A. 72, 152; Lewis, A. C. 423; Livingston, B. E. 147, 148, 292; Lyon, F. M. 124, 170, 376, 433; Macallum, A. B. 72; Moore, G. T. 309; Oliver, G.W. 306; Overton, J. B. 434; Preston, Carleton E. 35; Rehder, Alfred 56; Robertson, Charles 367; Schneck, J. 305; Schneider, Albert 142; Shull, G. H. 343; Smith, F. Grace 332; Stevens, F. L. 77, 157, 238; Thomas, M. B. 373; Wilcox, E. M. 226.

Cook, O. F., personal 154, 156; work of 434

Copeland, E. B. 356; personal 74

Corbett, L. C., personal 156; work of 151

Cornu, Maxime, death of 154; personal 443

Cornus, Small on 71

Corydalis aurea 106

Coulter, J. M. 62, 70, 153, 371, 373, 374, 375, 377, 426, 427, 428, 429, 430, 431, 432, 434, 435

Coulter, Stanley, work of 429

Coville, Frederick V., personal 155; work of 434

Cowles, H. C. 374, 376, 429, 430, 431; personal 74

Crataegus, Ashe on 68; Britton on 71; Sargent on 71; Small on 377

Crapulo, Miehe on 377

Croton, species of the U. S., Ferguson on 428; Texensis 289

Crystals, function of calcium oxalate 142

Cucurbita Pepo 367; Longo on 63

Cryptogams of Indiana, Thomas on 428

Curima, Cook on 435

Cuscuta, Rydberg on 378

Cylicomorpha, Urban on 71

Cynanchoideae, pollen of 325

Cynanchum vincetoxicum, Strasburger on pollen in 433

Cyperaceae, Meinshausen on 434

Cytology, of Albugo 77, 157, 262; of Cyanophyceae 72

D

Dale, Elizabeth, work of 375

Dalla Torre and Harms's "Genera Siphonogamarum" 62

Dandeno, J. B. 229, 439; personal 307

Dasylirion Texanum 288, formation 283

Dasystoma flava, Small on 378

Davis, B. M. 61, 63, 64, 222; work of 152

Dawson, Maria, work of 375

DeCandolle, C., Work of 71

Dennis, D. W., work of 428

Denniston, R. H., personal 443

Dewey, Lyster F., personal 156

Deyeuxia, Suksdorf on 377

Diatoms of Africa, Comber on 430

Dicerandra, Harper on 378

Dictyocephalos, White on 378

Dioscorea sativa, aerial tubers in 375

Diospyros *Texana*, Small on 378

Diseases, black locust, von Schrenk on 428; oat-smut, Shamel on 64; sear blight, Chester on 151; root-rot of fruit trees, Wilcox on 226; rusts of N. Am. violets, Arthur and Holway on 374; smut, Thomas on 428; tomato, Stuart on 429

Dorner, Herman B., personal 443

Draba cuneifolia 106; Greene on 377

Drymocallis, Rydberg on 70

Duggar, B. M., personal 156

Durand, work of 377; and Wildeman's "Reliquiae Deweveanae" 373

Dusén, work of 375

E

Earle, Frank S., personal 379; work of 70, 377

Eastwood, Alice, personal 228; work of 70

Echinocactus Wislizeni, anatomy of 44; assimilative tissue of 38

Echium vulgare, fasciation of 344

Ecology of Texas, 99, 195, 262

Ehretia elliptica 268

Embryo of Balanophoraceae, Chodat and Bernard on 70; of Nelumbo, Lyon on 374; of Selaginella spinulosa 171; protoplasmic continuity in 224

Embryo-sac of Lilium candidum, Bernard on 153

Endodermis of Osmundaceae 396

Endosperm, of Sequoia sempervirens 223; protoplasmic continuity in 224

Engler, A., work of 71; "Pflanzenreich" 427

Equisetum, Suksdorf on 377

Eremosphaera viridis 309

Erigeron Canadense, fasciation of 343
Ergot, Griffiths on 153
Ernst, work of 434
Eupatorium, boreale, Greene on 71; brevipes 422; Robinson on 153
Evax prolifera 106
Excentrosphaera viridis 320
Experiment station in Porto Rico 227

F

Fairchild, David G. 218; personal 156
Fanning, W. G., work of 374
Farlow, W. G., personal 227
Fasciation 343
Faull, J. H. 381
Fedde, Fr., work of 378
Fendlera rupicola 263
Ferguson, A. M., work of 428
Ferguson, Margaret C., 435
Fernald, M. L., 359; work of 153
Ferns, Christ on 153
Fertilization, double in Zea Mays 69; in Albugo 77, 157, 238; in Ginkgo biloba, Ikeno on 68; in Selaginella apus 131; Strasburger's theory of 240
Fitting, work of 174
Fistulinella, Hennings on 70
Flahault, work of 376
Flora, of Indiana, Coulter on 429; of Isle Royale, Wheeler on 374; of Lake Maxinkuckee, Scovell on 428; of North Dakota, Bolley and Waldron on 68; of Oklahoma, Bogue on 68; of Porto Rico, Underwood on 443; of Red River Valley, Wheeler on 374; of South Dakota, Saunders on 6; of S. E. Tennessee, Coulter on 429; of West Indies, Britton on 443; of Yukon, Britton and Rydberg on 72
Flowers, abnormal 346; and insects 367
Fouquiera splendens 276, 284
Forest, a tropical in Ceram 218; formations 211, 262, 266; xerophytic 215
Forti, Achille, work of 71
Frankenia Jamesii 287
Frasera speciosa 263
Fraxinus Berlandieriana 268
Freeman, E. M., work of 374
Friedel, work of 430
Frye, T. C., 325, 433
Fungi, from Porto Rico, Earle on 70, 377; Henning on 70; Massee on types of 378; of Africa, Smith on 430; of west America 444
Fungicides, effect on foliage, Sturgis on 66

G

Galloway, Beverly T., personal 155, 228
Gametogenesis in Albugo 77, 157, 238
Gametophytes of Selaginella 124, 170
Ganong's "Laboratory course in plant physiology" 148
Garden, New York Botanical 75
Garden beans, Irish on 428
Gardner, N. L., personal 155
Garman, H., work of 67
Gattinger's "Flora of Tennessee" 428
Generic nomenclature of cedar apples, Arthur on 428
Geneva convention 307
Gentiana, Holm on 377
Geotropism, Giesenhagen on 432
Gepp, Antony, work of 430
Geranium caespitosum 263
Gesneriaceae, Urban on 431
Gibson and Auld's "Codium" 63
Giesenhagen, work of 432
Gigartina exasperata. Humphrey on 374
Gilbert, Benjamin D., work of 429
Gilg, E., work of 70, 71
Gilbert, B. D., work of 71, 377
Goebel, work of 178
Goff, E. S., work of 64
Gow's "Flowering plants of Adair county, Iowa" 373
Gould, H. P., personal 156
Gramineae, Pilger on 71
Grass formations 118, 196, 198, 204, 207, 271
Grasses, of Iowa, Pammel and Weems on 429; of Kansas, Hitchcock on 67; of Kentucky, Garman on 67
Gray, Asa, memorial tablet to 75
Greasewood formation 275
Greene, E. L., work of 71, 153, 377
Griffiths, David, personal 156, 444; work of 153; "North American Sordariaceae" 427
Griggs, Robert F., personal 154
Growth, Nabokich on anaerobic 435; periodicity of in Cactaceae 42, 55
Gruber, Eduard, work of 66
Gutierrezia Texana 289

H

Hall, H. M., personal 155
Hallier, Hans, work of 431
Hallowell, Miss S. M., personal 379
Halophytic vegetation 286
Halsted, B. D., personal 228
Hapalophragmium, Sydow on 378
Harkness, H. W., death of 154

Harms, H., work of 71; and Dalla Torre's "Genera Siphonogamarum" 62
Harper, R. M., work of 378
Harshberger, J. W., work of 429
Hasselbring, H., personal 154
Havardia, Small on 71
Hedlund's "Monographie der Gattung Sorbus" 373
Hedophyllum, Setchell on 70, 153
Hefferan, Mary 370
Heisen, work of 172
Helosis guayanensis, Chodat and Bernard on 70
Hemlock, water, Brodie on 68
Henderson, L. F., work of 65
Hennings, P., work of 70
Herbarium, committee on national 380; of von Heldreich, 379
Hesselman, work of 376
Heteroceras, Forti on 71
Heuchera rubescens 263
Hibiscus lasiocarpus 367
Hicoria, branched leaf of 345
Hieracium, Britton on 153
Hilaria Jamesii formation 201
Hill, A. W., work of 224
Histology of Osmundaceae 385
Hitchcock, A. S., personal 156; work of 67
Hollick, A., personal 228
Holm, Theo., work of 377
Holodiscus 57
Holway, E. W. D. 421, 422; work of 374
Hooker, Sir J., personal 380
Horkelia, Rydberg on 70
Hottes, Chas. F., personal 154
Howe, Marshall A., personal 154; work of 70, 71
Humphrey, H. B., work of 374
Husmann, George C., personal 156
Hyams, C. W., work of 65
Hybridity in palms, Waugh on 68
Hydnum, Banker on 153
Hypoderma of Cactaceae 37
Hyptiodaphne, Urban on 431

I

Ianthe, Williams on 434
Ikeno, work of 68
Ilex opaca, middle lamella of 23
Indiana, Coulter on flora of 429
Inodes, Cook on 435
Insects and flowers 367
Intercellular substance 2
Ipomoea pandurata 367
Irish, H. C., work of 428

J

Jatropha, macrorhiza 122; spathulata 122
Jepson, W. L., personal 155
Johnson, D. S., personal 154
Johnson, T. C. 303
Juglans, nigra 111; rupestris 111
Juncoides, Small on 377
Juncus, Suksdorf on 377
Juniperus, monosperma 216; occidentalis 216; pachyphloea 216, 262; sabinoides 111, 212; formation 213; Virginiana 111, 213

K

Kahlenberg, Louis 437
Karyokinesis, physiology of 423
Kearney, Thomas H., personal 156
Koehnela, Urban on 431
Kofoid, C. A., work of 150
Kolkwitz, work of 431
Komarov, V. L., work of 434
Kraemer, Henry 423
Krameria secundiflora 198
Krigia amplexicaulis 367

L

Laboratory, botanical, of Glasgow University 379; and gardens of Tokyo Imperial University, Miyake on 379
Lacinaria, Greene on 377
Lactariopsis, Hennings on 70
Lamella, origin and nature of the middle 1
Laminariaceae, Setchell on 70
Lamson-Scribner, F., personal 155; work of 71; "American grasses, II" 62
Land, W. J. G. 69
Lang, W. H., work of 376
Lange, D., work of 374
Larrea Mexicana 287, formation 275
Lathyrus odoratus, abnormal flowers 346
Lauraceae, Mez on 71
Lawson, A. A. 72, 152; personal 74, 227
Leaf trace of Osmundaceae 400
Leaves, abnormal 345
Leersia oryzoides, DuSablon on 67
Leguminosae, Harms on 71
Lepidodendron Braunii 179
Lepidostrobus Veltheimianus 179
Leptilon Canadense, fasciation of 343
Lesquerella, Greene on 377
Lespedeza, Bicknell on 377
Leucophyllum Texanum formation 274
Lewis, Arthur Carr 423; personal 228
Liatris pycnostachya 198

Lichens of Africa, Wainio on 430
Linaria, Canadensis 106; spuria, Du Sablon on 67
Lindau, G., work of 71
Lister, Arthur, work of 430
Liverworts, Howe on 71; of Africa, Stephani on 430, 431
Livingston, B. E., 147, 148, 292
Longo, B., work of 63
Lopriore, G., work of 71, 377
Lycopus, Steele on 434
Lyon, F. M. 124, 170, 376, 433; personal 227
Lyon, Harold, personal 155; work of 374
Lysimachia terrestris, MacDougal on 65
Lupinus subcarnosus 210, 273

M

Macallum, A. B. 72
MacDougal, D. T., personal 227, 228; work of 65; "Textbook of plant physiology" 148
Macmillan, Conway, personal 155
Magnolia grandiflora 111
Mahonia, Fedde on 378
Makino, T., work of 153
Malformations 343
Mamillaria Grahami, anatomy of 48
Marine algae of Africa, Barton on 430
Massee, George, work of 378
Masters, Maxwell T , work of 153
Matsumura, J., work of 377
Medulla of Cactaceae 39; of Osmundaceae 397
Medullary rays, middle lamella of 18
Meehan, Thomas, death of 443
Megasporangium, of Selaginella apus 131; of S. rupestris 138
Megaspore, of Selaginella apus 126; of S. rupestris 138
Meinshausen, K. Fr., work of 434
Meissner, work of 356
Melampodium, Robinson on 153
Meliaceae, De Candolle on 71
Melica, Suksdorf on 377
Memorial tablet, to Asa Gray 75; to T. C. Porter 74
Merrill, Elmer D., personal 156; work of 71
Mesquite formation 272
Mesogamy, Longo on 64
Mexico, Fernald on plants of 153; Robinson on plants of 153
Mez, Carl, work of 71, 431
Microsporangium, of Selaginella apus 135; of S. rupestris 139
Microspore, of Selaginella apus 132; of S. rupestris 139
Miehe, H., work of 377
Millardet, work of 175, 177
Mimosaceae, Small on 71
Mimoseae 268
Minnesota, Botanical Studies 374; Seaside Station 155
Mistletoe, Wheeler on dwarf 68
Mitosis, simultaneous 241
Miyake, Kiichi, work of 379
Mohr, Charles, death of 227; bibliography of 379; sketch of 443; "Plant life of Alabama" 371
Molisch's "Milchsaft und Schleimsaft" 369
Monarda, Rydberg on 378
Moore, G. T. 309; personal 74, 156
Mosses, of Africa, Gepp on 430; of Greenland, Dusén on 375; of Yukon, Williams on 72; on trees 422
Mucorineae, phylogeny of 164
Murrill, W. A., personal 228
Mushrooms, Henderson on 65; Hyams on 65
Mycetozoa of Africa, Lister on 430
Mycological notes, Williamson on 429
Mycorhiza of arctic plants, Hesselman on 376
Myrsinaceae, Gilg on 71; Mez on 431
Myxoderma, Schmidle on 378

N

Nabokich, work of 435
Naturalists, meeting of 444
Needles, Meisner on 356
Neljubow, D., work of 151
Nelson, Aven, personal 228; work of 68, 153
Nelson, Elias, work of 434
Nelson, N. L. T., personal 307
Němec, work of 375; "Die Reizleitung und die reizleitenden Strukturen" 146; "Wahrnehmung des Schwerkraftreizes" 145
Nemophila, Eastwood on 70
Nerium oleander, middle lamella of 17
Nitragin, Dawson on 375
Nocca, Robinson on 153
Nomenclature 421; instability of Rochester 359
Notoptera, Urban on 431
Nucleus of Pellia, Davis on 152
Nutation of peas, Neljubow on 151

O

Oak, formation of live 265; formation of post 264; Rydberg on 72
Oat smut, Shamel on 64

Oenothera biennis 367
Oliver, G. W. 306
Oogenesis in Albugo 159
Opuntia, arborescens 279; arbuscula, anatomy of 50; frutescens 279; fulgida, anatomy of 49; leptocaulis, anatomy of 51; assimilative tissue of 38; Lindheimeri formation 274, 278; phaeacantha, anatomy of 49
Orchis mascula 329
Orton, Wm. A., personal 156
Osmotic pressure, effect on form 292
Osterhout, W. J. V., personal 155
Osmundaceae, anatomy of 381
Overton, J. B. 434; personal 74
Oxalis acetosella, Du Sablon on 67

P

Palisade tissue of Cactaceae 38
Palmetto, Trelease on a Pacific 428
Palms, Cook on 434
Pammel, L. H., personal 228; work of 68, 430
Panicularia, Beal on 153
Panicum, Ashe on 68; Lamson-Scribner and Merrell on 71
Papilla, receptive 245
Paraguay, Chodat on new plants of 71
Parkinsonia, aculeata 103, 111; Texana 272, formation 274
Patterson, Flora W., personal 156
Pear blight, Chester on 151
Pectose 4
Peirce, G. J., personal 74
Pelargonium, abnormalities in 345
Pellaea, Trelease on a cristate 428; atropurpurea, Trelease on 71
Pellia, Davis on nucleus of 152
Pentstemon, Rydberg on 378
Pericycle of Osmundaceae 386
Periplocoideae, pollen of 325
Peronospora parasitica 161
Peronosporaceae, phylogeny of 164
Persea Borbonia 111
Personals: Allen, C. E. 443, 444; Anderson, A. P. 154, 379; Arthur, J. C. 74, 228; Autran, E. 227; Balfour, B. 380; Ball, C. R. 156; Beal, W. J. 228; Bergen, J. Y. 307; Bessey, C. E. 74, 228; Bessey, E. A. 156; Bower, F. O. 227; Brackett, G. B. 155; Britton, E. G. 228; Britton, N. L. 75; Bureau, E. 443; Butler, Eloise 155; Campbell, D. H. 228; Carleton, M. A. 156; Chamberlain, J. H. 156; Chesnut, B. K. 156; Clements, F. E. 75, 228; Clinton, G. P. 154; Collins, G. M., 154; Cook, O. F. 154, 156; Copeland, E. B. 74; Corbett, L. C. 156; Cornu, M. 154, 443; Coville, F. V. 155; Cowles, H. C. 74; Dandeno, J. B. 307; Denniston, R. H. 443; Dewey, L. F. 156; Dorner, H. B. 443; Duggar, B. M. 156; Earle, F. S. 379; Eastwood, Alice 228; Fairchild, D. G. 156; Farlow, W. G. 227; Galloway, B. T. 155, 228; Gardner, N. L., 155; Gould, H. P. 156; Gray, Asa 75; Griffiths, D. 156, 444; Griggs, R. F. 154; Hall, H. M. 155; Hallowell, Susan M. 379; Halsted, B. D. 228; Harkness, H. W. 154; Hasselbring, H. 154; Hitchcock, A. S. 156; Hollick, A. 228; Hooker, Sir J. 380; Hottes, C. F. 154; Howe, M. A. 154; Husmann, G. C. 156; Jepson, W. L. 155; Johnson, D. S. 154; Kearney, T. H. 156; Lamson-Scribner, F. 155; Lawson, A. A. 74, 227; Lewis, A. C. 228; Lyon, F. M. 227; Lyon, H. L. 155; MacDougal, D. T. 227, 228; MacMillan, C. 155; Meehan, T. 443; Merrill, E. D. 156; Mohr, C. 227, 379, 443; Moore, G. T. 74, 156; Murrill, W. A. 228; Nelson, A. 228; Nelson, N. L. T. 307; Orton, W. A. 156; Osterhout, W. J. V. 155; Overton, J. B. 74; Pammel, L. H. 228; Patterson, Flora W. 156; Peirce, G. J. 74; Philibert, H. 74; Pierce, N. B. 156; Pieters, A. J. 156; Porter, T. C. 74, 379; Ramaley, F. 155, 228; Robinson, B. L. 75, 228; Rolfs, P. H. 156; Rose, J. N. 76, 307; Ruger, Mrs. G. J. 443; Schiffner, V. 443; Schimper, A. F. W. 379; Schofield, C. S. 156; Schrenk, H. von 75, 156, 228; Selby, A. D. 228; Setchell, W. A. 155; Shaw, W. R. 443; Shear, C. F., 156; Shepard, C. U. 156; Slosson, E. E. 228; Smith, E. F. 155; Solereder, Hans 443; Stevens, F. L. 154; Stuart, W. 443; Stuntz, S. C. 444; Swingle, W. T. 155; Taylor, W. A. 156, 228; Thaxter, R. 379; Thornber, J. J. 75; Timberlake, H. G. 443; Townsend, C. O. 156; Trelease, W. 228; True, R. H. 156; Underwood, L. M. 154, 228; Waite, M. B. 156; Webber, H. J. 156; West, W. 379; White, V. S. 228; Whitford, H. N. 74; Wilcox, E. M. 307; Williams, T. A. 444; Winkenwerder, H. A. 443; Woods, A. F. 155; Yendo, K. 155
Pfeffer, W., work of 171, 177
Philibert, Henri, death of 74
Phloem, of Osmundaceae 389; Weiss on 429

Photomicrography, Dennis on 428

Phycomycetes 167; phylogeny of 165

Phyllocomos, Masters on 153

Phylogeny, of Albuginaceae 157; of Mucorineae 164; of Osmundaceae 415; of Peronosporaceae 164; of Phycomycetes 165; of Saprolegniaceae 164

Phytogeography, Flahault on nomenclature in 376

Picea, needles of 356

Pierce, Newton B., personal 156

Pieters, A. J., personal 156

Pilger, R., work of 71, 431

Pinus, edulis 216, 262, 263; Ferguson on 435; flexilis 106, 262; needles of 356; palustris 111; ponderosa 106, 262; silvestris, middle lamella of 12; protoplasmic continuity in 224

Piper and Beattie's "Flora of the Palouse region" 62

Piperaceae, DeCandolle on 71

Piperia, Rydberg on 71

Pith cells, middle lamella of 20

Plankton, Kofoid on 150; Ward on 150

Plants of Isle Royale, Wheeler on 374; of North Dakota, Bolley and Waldron on 68; of Oklahoma, Bogue on 68; of South Dakota, Saunders on 6; of southeastern Tennessee, Coulter on 429; Rostowzew on drying 306

Pleurococcus on trees 422

Pleurophycus, Setchell on 70, 153

Plums, Waugh on hybridity in 68

Pollen, development of 325; Strasburger on formation of 433; tube, Longo on 63

Populus Fremontii 268

Polyembryony in Tulipa Gesneriana, Ernst on 434

Porter, Thomas Conrad, memorial tablet to 74; biography of 370

Potamogeton, polygonifolius in Newfoundland, 58, synonymy of 59; Suksdorf on 377

Potentilla, Rydberg on 70

Pound and Clements's "Phytogeography of Nebraska" 374

Preston, Carleton E. 35

Primula, Rydberg on 378

Prizes, Walker 380

Prosopis juliflora 105, 111, 198, 270; formation 272

Protarum, Engler on 71

Proteids, Jost on synthesis of 429

Pseudomonas, Smith on 430

Pseudotsuga taxifolia 106, 262

Ptelea, Small on 71

Pteridophytes, Carruthers on African 430; North American, Gilbert on 429; of Iowa, Shimek on 153; of Yukon, Underwood on 72

Pteris aquilina 391; middle lamella of 10

Puccinia, Circaeae 421; graminis 421; inanipes 422; Malvacearum 421

Pyronema 167

Q

Quercus, breviloba formation 214; Emoryi 216, 263, 288; Gambelii 217; grisea 216; marilandica 264; minor 264; undulata 217; Virginiana 266; formation 214

R

Ramaley, Francis, personal 155, 228

Rehder, Alfred 56

Respiration, intramolecular 303; of barley, Kolkwitz on 431

Restionaceae, Masters on 153

Revegetation of Trestle island, Lange on 374

Reviews: Arnold's "The sea beach at ebb-tide" 222; Bessey's "Structure and classification of diatoms" 150; Britton's "Manual of the flora of the northern states and Canada" 426; Chamberlain's "Methods in plant histology" 372; Chester's "Manual of bacteriology" 370; Church's "Phyllotaxis" 427; Dalla Torre and Harm's "Genera Siphonogamarum" 62; Engler's "Pflanzenreich" 427; Ganong's "Laboratory course in plant physiology" 148; Gattinger's "Flora of Tennessee" 428; Gibson and Auld's "Codium" 63; Gow's "Flowering plants of Adair county, Iowa" 373; Griffith's "North American Sordariaceae" 427; Hedlund's "Monographie der Gattung Sorbus" 373; Lamson-Scribner's "American grasses II" 62; MacDougal's "Text-book of plant physiology" 148; Mohr's "Plant life of Alabama" 371; Molisch's "Milchsaft und Schleimsaft" 369; Němec's "Wahrnehmung des Schwerkraftreizes" 145, "Die Reizleitung und die reizleitenden Strukturen" 146; Piper and Beattie's "Flora of the Palouse region" 62; Pound and Clements's "Phytogeography of Nebraska" 374; Robinson's "Problems and possibilities of systematic botany" 432; Sturgis's "Literature of plant diseases" 65; Thonner's "Excursionsflora von Europa" 428; Urban's "Symbolae Antillanae" 431; von Schrenk's "Factors

which cause the decay of wood" 62; Weathers's "Guide to gardenplants" 306; Wettstein's "Handbuch der systematischen Botanik" 61; Weisner's "Rohstoffe des Pflanzenreiches" 373; Wildeman and Durand's "Reliquiae Dewevreanae" 373; Wille's "Studien über Chlorophyceen" 64
Rhizoids of Chara, Giesenhagen on 431
Rhizome of Osmundaceae 384
Rhodoplax, Schmidle and Wellheim on 377
Rhynchospora, Harper on 378
Rhynchotropis, Harms on 71
Ribes viscosissimum 263
Riccia, Howe on 70
Richards, H. M., work of 71
Robertson, Charles 367
Robinson, B. L., personal 75, 228; work of 153; "Problems and possibilities of systematic botany" 432
Rock vegetation 284
Rocky mountains, Rydberg on new plants of 71
Rolfs, Peter H., personal 156
Root, of Cereus Fendleri 42; Němec on plagiotropous 375; of Osmundaceae 401; perception and propagation of stimuli in 145; rot of fruit trees, Wilcox on 226
Rosa, middle lamella of 20
Rose, J. N., personal 76, 307
Rostowzew, work of 306
Roze, work of 176
Rudbeckia, Small on 377
Ruger, Mrs. G. J., personal 443
Rumex, Greene on 377
Rusts, of North American violets, Arthur and Holway on 374
Rydberg, P. A., work of 70, 71, 72, 378

S

Salix, Ball on 434; Coville on 434
Sabal, Mexicana 268; *Uresana* 428; Trelease on 153
Sambucus, Rydberg on 378
Saprolegnia 161
Saprolegniaceae 244; phylogeny of 164; oogenesis in 163
Sargent, C. S., work of 71; "Silva of North America" 443
Sasa, Makima and Shibata on 153
Saunders, D. A., work of 68, 374
Schefflerodendron, Harms on 71
Schiffner, V., personal 443
Schimper, A. F. W., death of 379
Schizonotus 56
Schizonotus 440; tomentosus 57
Schmidle, W., work of 70, 71, 377, 378
Schneck J., 305
Schneider, Albert 142
Schofield, Carl S., personal 156
Schrebera, Gilg on 70
Schrenk, H. von, personal 75, 156, 228; work of 428
Sclerenchyma, middle lamella of 10
Scorodophloeus, Harms on 71
Scott, work of 179
Scovell, J. T., work of 428
Seed, Billings on development 433; plants of Yukon, Britton and Rydberg on 72
Selaginella, lepidophylla 286; rupestris 286; sporangia and gametophytes of 124, 170
Selby, A. D., personal 228
Sequoia sempervirens, endosperm of 223
Sericostachys, Lopriore on 378
Setchell, W. A. personal 155; work of 70, 153
Shamel, A. D., work of 64
Shaw, W. R., personal 443
Shear, Cornelius F., personal 156
Shepard, Charles U., personal 156
Shibata, K., work of 153
Shimek, B., work of 153
Shrubs, Small on new 378
Shull, G. H. 343
Siderocarpos, Small on 71
Sieve tubes in Osmundaceae 390
Sisyrinchium, Bicknell on 435; Suksdorf on 377
Slosson, E. E., personal 228
Small, J. K., work of 71, 377, 378
Smith, Anna L., work of 430
Smith, E. F., personal 155; work of 430
Smith, F. Grace 332
Smut, Clinton on new species 71; Shamel on oat 64; Thomas on 428
Solanoa 57
Solanum, Carolinense, Pammel on 68; dulcamara, calcium oxalate in 142
Solereder, Hans, personal 443
Solutions, application of normal to biological problems 229, 437
Sorbaria 58, 440
Sphaeropsis malorum, Chester on 151
Sphaeralcea martii 60
Spiraea, *discolor* 57; *Lindleyana* 57; *sorbifolia* 56, 57; *Ulmaria* 58
Spirostachys occidentalis 287
Sporangia of Selaginella 124, 170
Sporobolus, airoides 287; cryptandrus 205; Wrightii 287
Sporodinia, Gruber on zygospore of 66
Sporophytes of Selaginella apus 136

Stamens, abnormal 351
Steele, E. S., work of 434
Stem of Osmundaceae 384
Stephani, F., work of 430, 431
Stevens, F. L., 77, 157, 238; personal 154
Stigeoclonium tenue, polymorphism in 292
Stomata of Cactaceae 37
Strasburger, work of 433
Stuart, Wm., personal 443; work of 429
Stuntz, Stephen C., personal 444
Sturgis, W. C., work of 66; "Literature of plant diseases" 65
Suaeda, depressa 287; suffruticosa 287
Succulents, formations 277
Suksdorf, W. N., work of 377
Swingle, W. T., personal 155
Sydow, H. & P., work of 378

T

Tammes, work of 431
Taxodium distichum 269
Taxonomy 70, 153, 377, 434
Taylor, Wm. A., personal 156, 228
Teratology 343
Tetraperone, Urban on 431
Teucrium, Bicknell on 70
Texas, ecology of western 99, 195, 262
Thaxter, Roland, personal 379
Thecanisia *discolor* 58
Theophrastaceae, Mez on 431
Thomas, M. B. 373; work of 428
Thonner's "Excursionsflora von Europa" 428
Thornber, John J., personal 75
Thrincoma, Cook on 435
Thringis, Cook on 435
Tilia americana, middle lamella of 22
Timber formations 266, 268
Timberlake, H. G., personal 443
Todea, anatomy of 382
Toumey, J. W., work of 71, 428
Townsend, C. O., personal, 156; work of 64
Trachyphyllum, Gepp on 430
Tracy, S. M., work of 379
Tragopogon 78
Trees, pleurococcus and mosses on 422; Small on new 378; of Vermont, Clark on, 68; of Wyoming, Nelson on 68
Trelease, William, personal 228; work of 71, 153
Tribulus, terrestris, Pammel on 68; aurantiacum, Bicknell on 70
Trifolium, Rydberg on 378
True, Rodney H., personal 156
Tubers, Dale on aerial 375
Tulipa Gesneriana, Ernst on polyembryony in 434
Tylostomaceae, White on 378
Typha latifolia 329

U

Ulmaria, pentapetala 58; rubra 58
Underwood, L. M., personal 154, 228; work of 72, 443
Urban, I., work of 71, 431; "Symbolae Antillaneae" 431
Uredineae, Freeman on Minnesota 374
Uredo, cestri 422; Hydrocotyles 422

V

Variation, Harshberger on limits of 429
Vascular system of Cactaceae 40
Vexillum, abnormal 351
Viola, Greene on 377; Harper on 378; odorata, DuSablon on 67; Steele on 434
Vicia, Rydberg on 378
Von Schrenk's "Factors which cause the decay of wood" 62

W

Wainio, E. A., work of 430
Waite, Merton B., personal 156
Waldron, L. R., work of 68
Wallrothiella Arceuthobii 65
Ward, Henry B. 150
Water, storage of 36
Waugh, F. A., work of 68
Weathers's "Guide to garden plants" 306
Webber, H. J., personal 156
Weeds, Pammel on 68
Weeksia, Setchell on 70, 153
Weems, J. B., work of 430
Weiss, F. E., work of 429
Wellheim, work of 377
West, William, personal 379; work of 430
Wettstein's "Handbuch der systematischen Botanik" 61
Wheeler, C. F., work of 64, 68, 374
Whipple, George C., work of 150
White, V. S., personal 228; work of 378
Whitford, H. N., personal 74
Wiesner's "Rohstoffe des Pflanzenreiches" 373
Wilcox, E. Mead 226; personal 307; work of 226
Wildeman, work of 377; and Durand's "Reliquiae Dewevreanae" 373
Wille, "Studien über Chlorophyceen" 64
Williams, R. S., work of 72
Williams, F. N., work of 434

Williams, Thomas A., personal 444
Williamson, E. B., work of 429
Willows, Ball on 434; Coville on 434
Winkenwerder, H. A., personal 443
Woods, Albert F., personal 155
Wyoming plants, Nelson on 153

X

Xylariaceae, Butten on Minnesota 374
Xylem, middle lamella of 13, 17; of Cactaceae 41; of Osmundaceae 386

Y

Yamanouchi, S., work of 374
Yendo, K., personal 155
Yucca,-agave-cactus formation 282; angustifolia 204; formation 288; glauca 271; macrocarpa, formations 283; rupicola 198; vegetation 280

Z

Zea Mays, double fertilization in 69
Zygospore of Sporodinia, Gruber on 66

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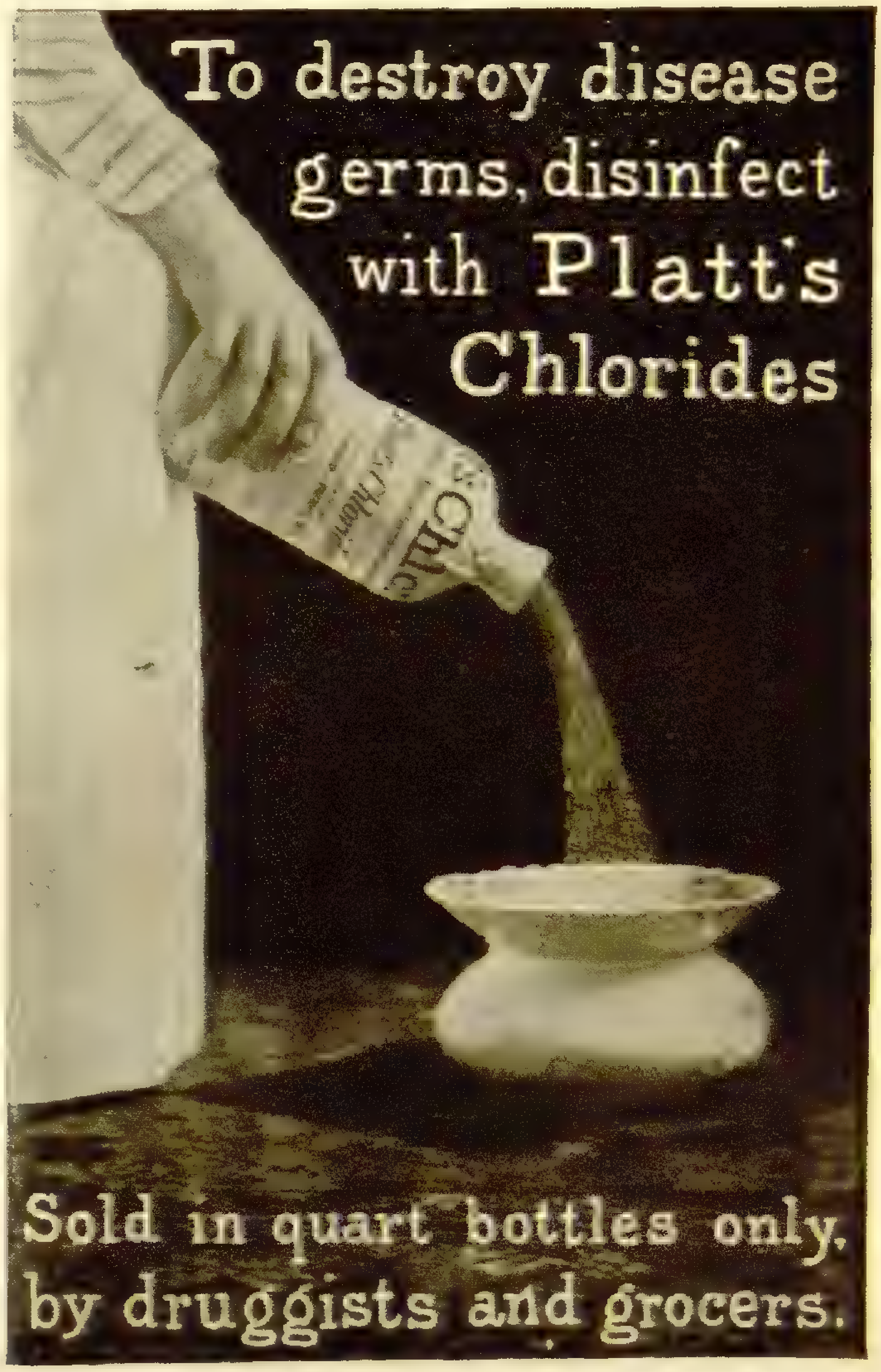
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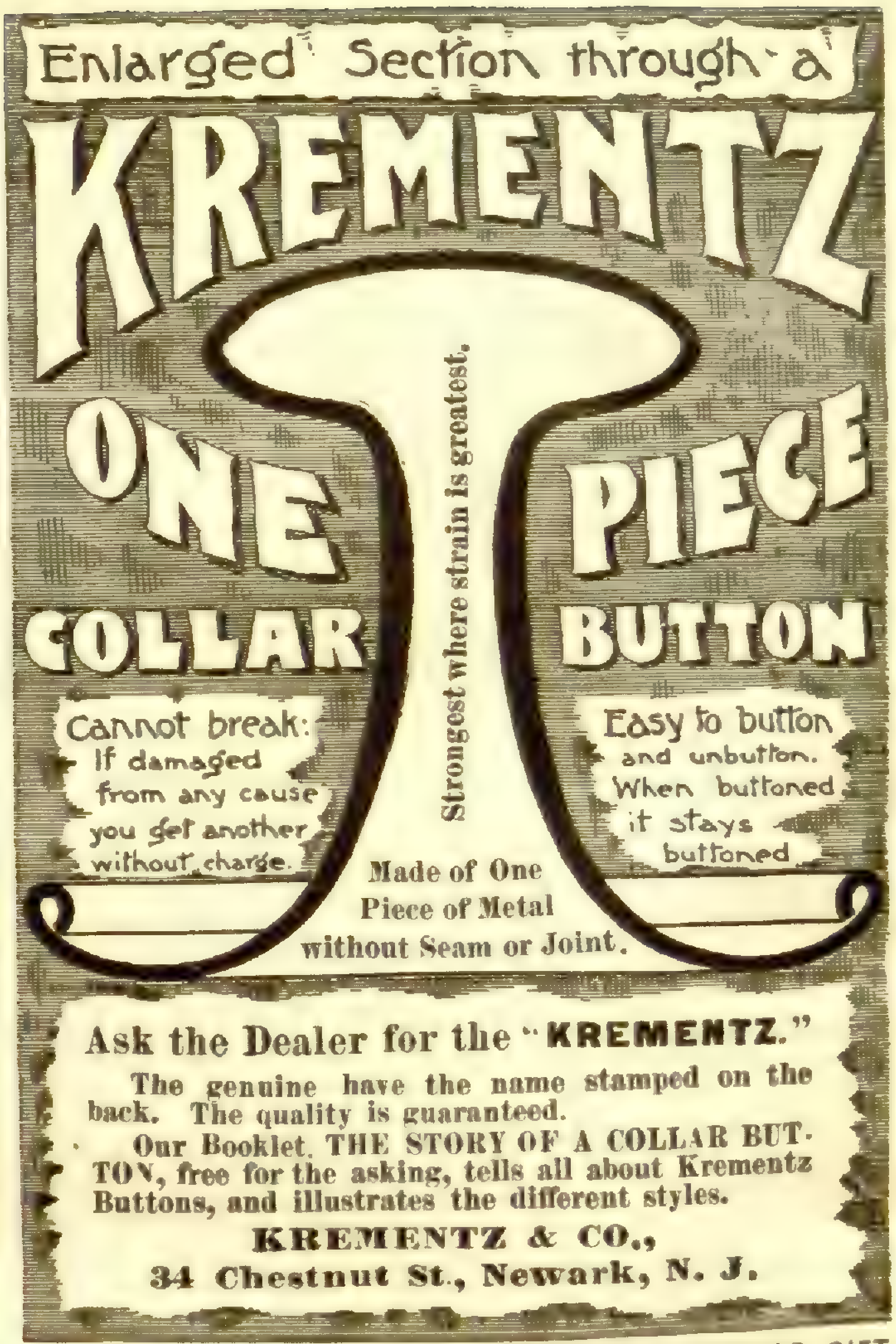

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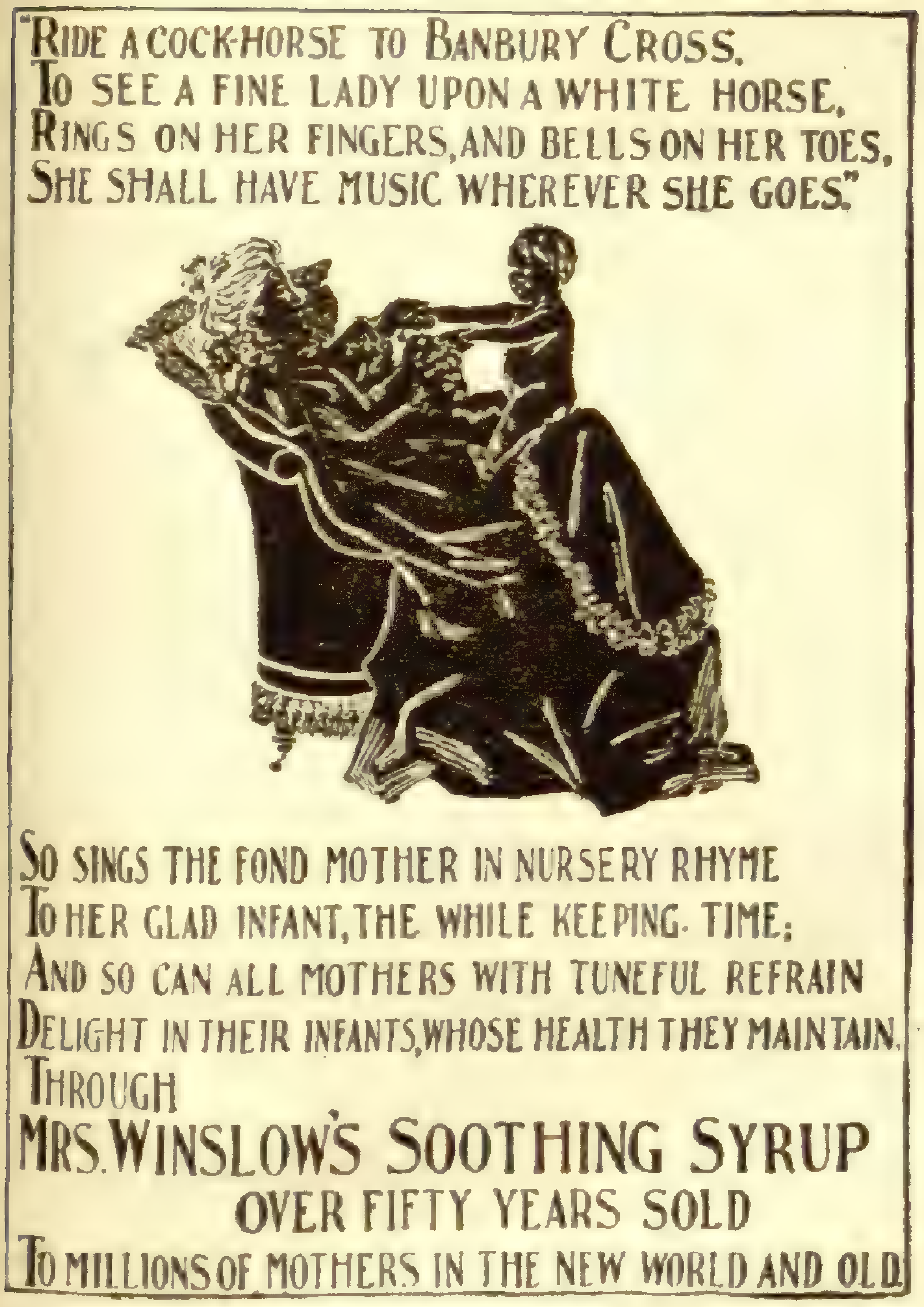
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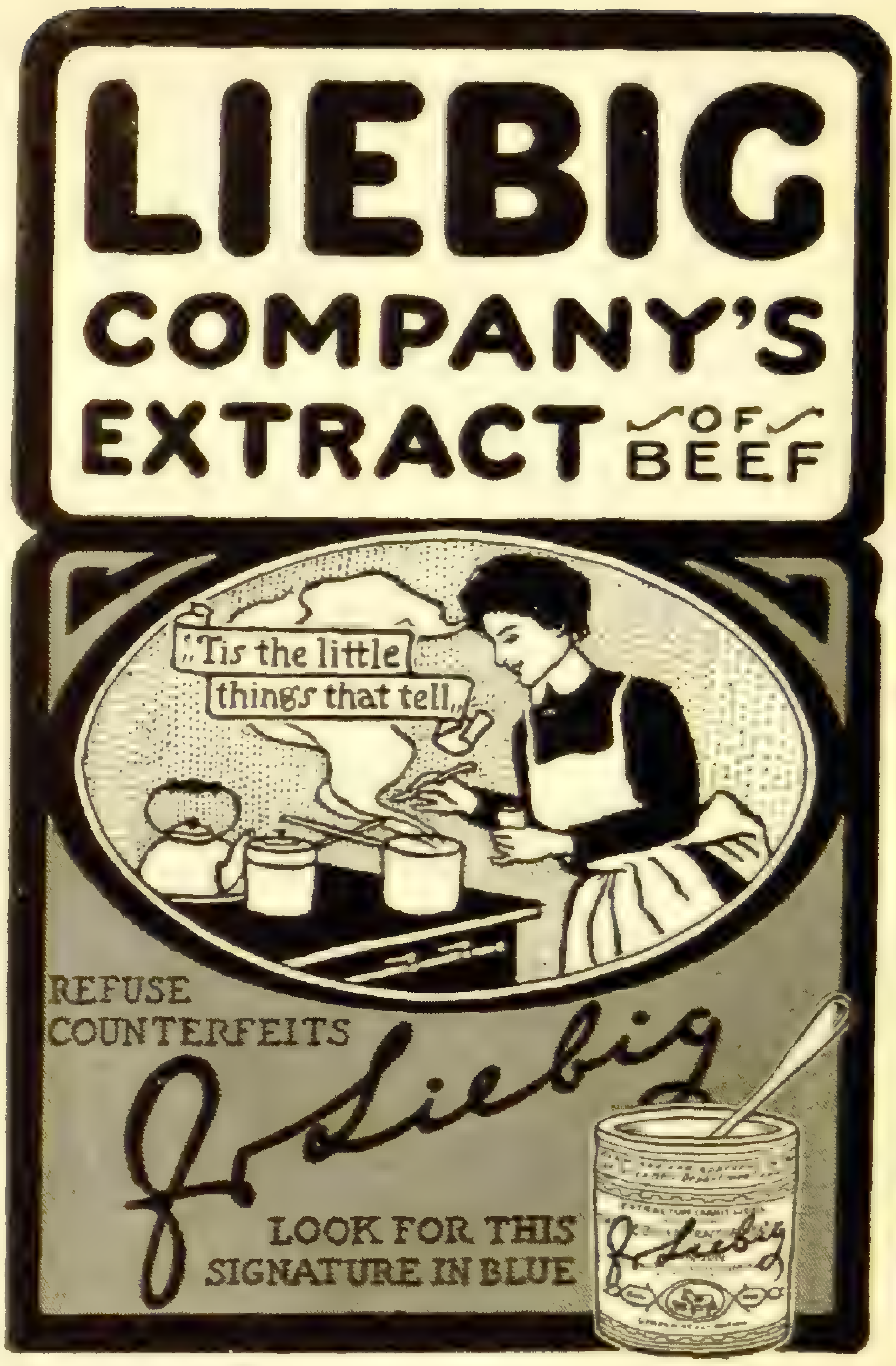
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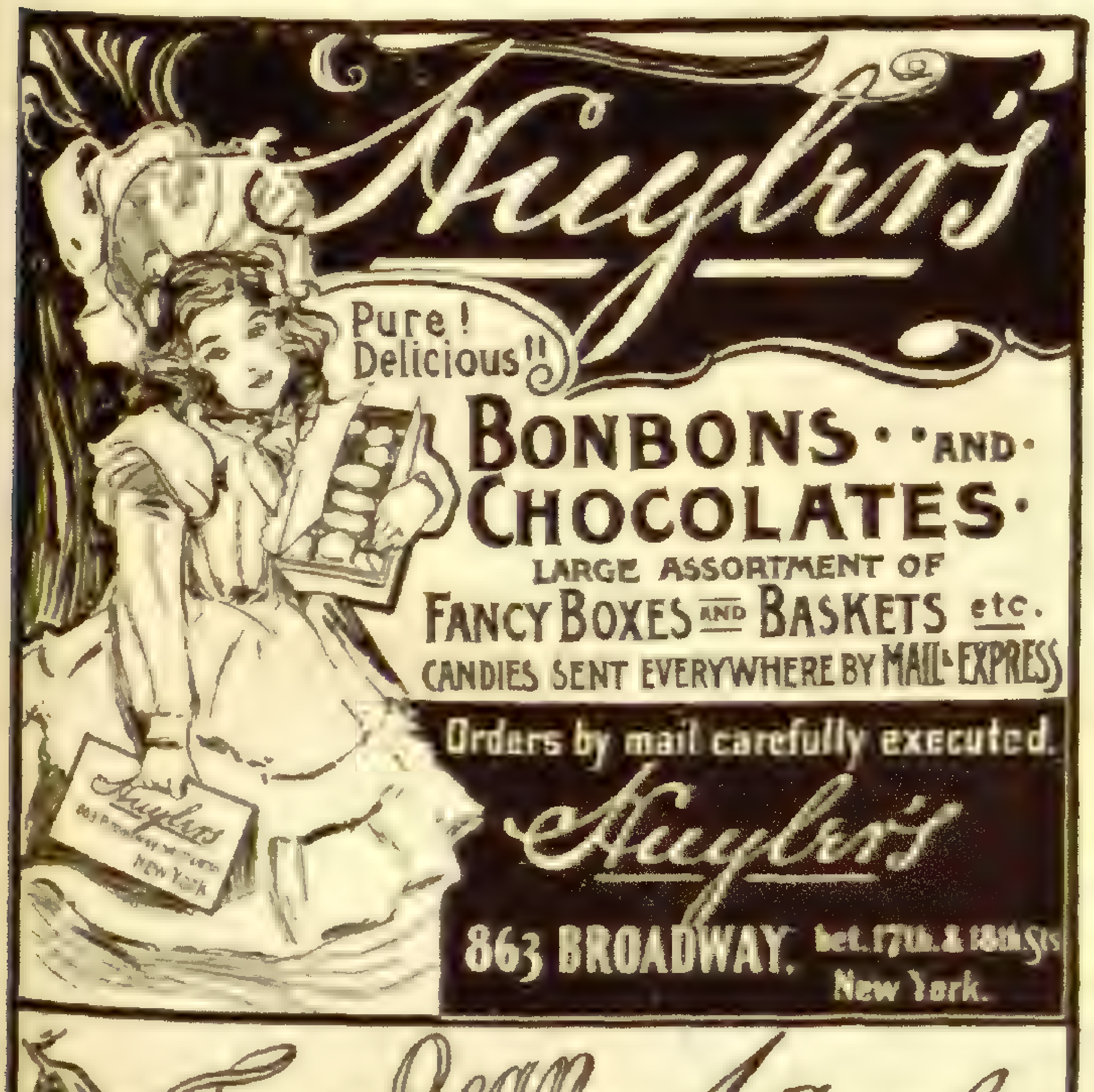
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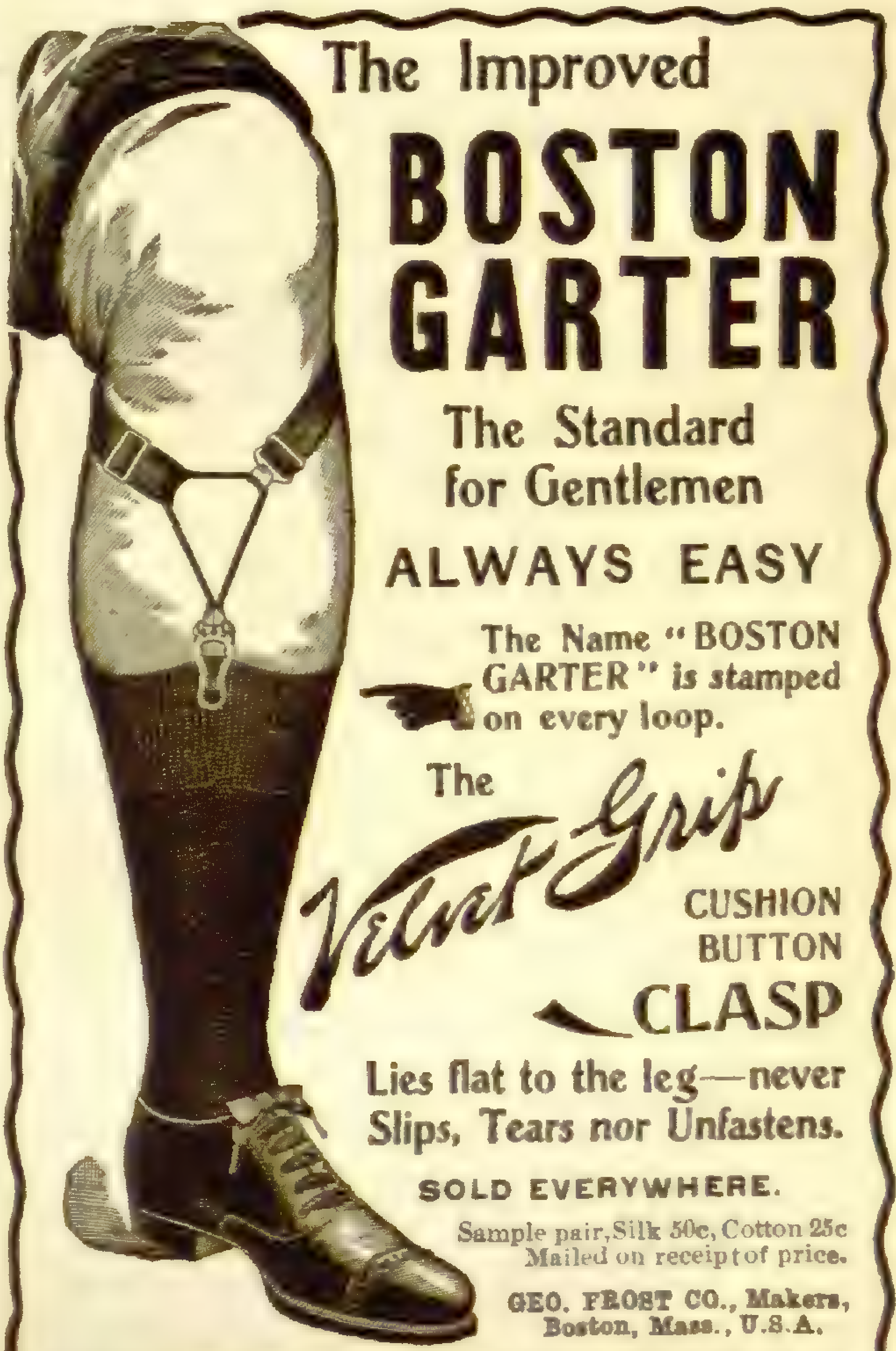
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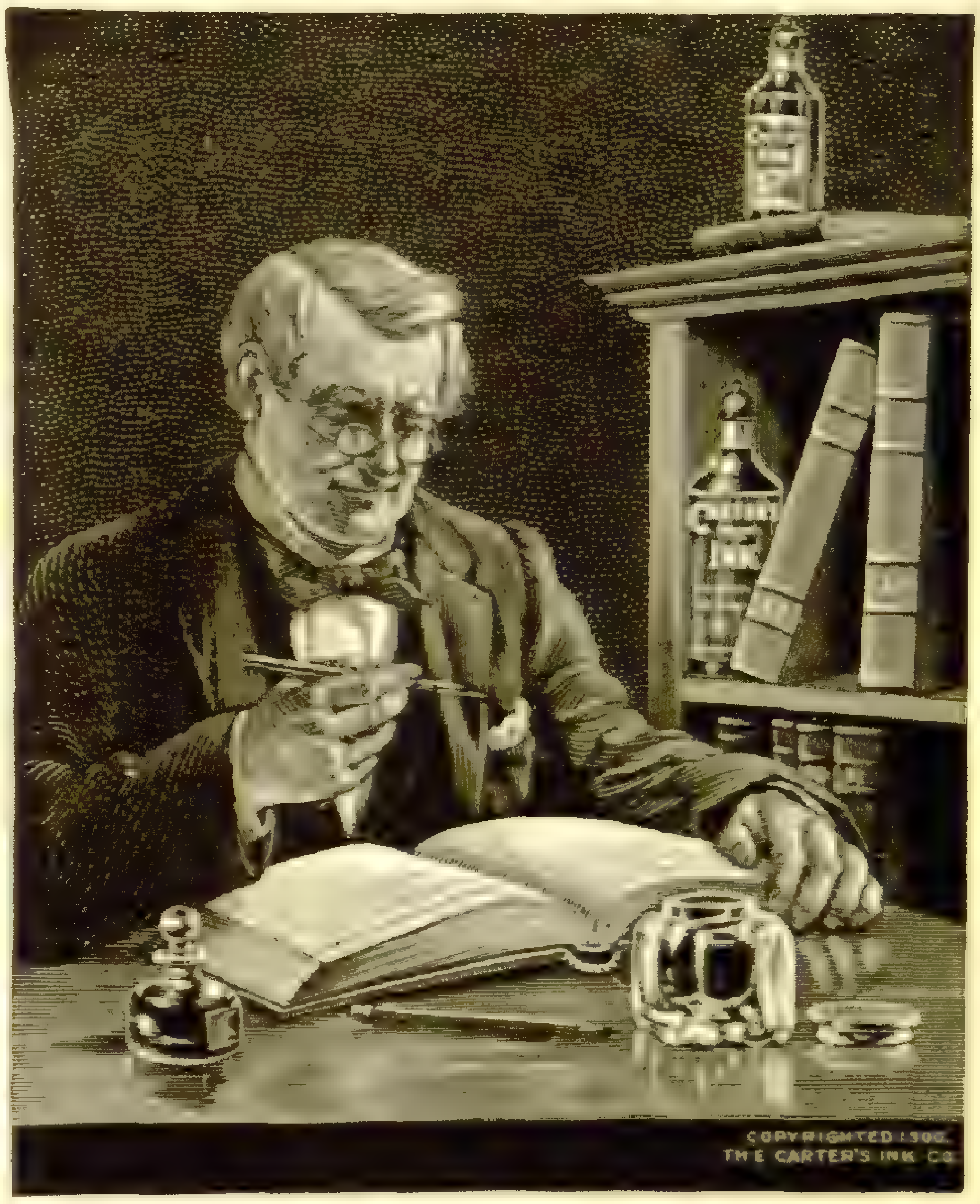
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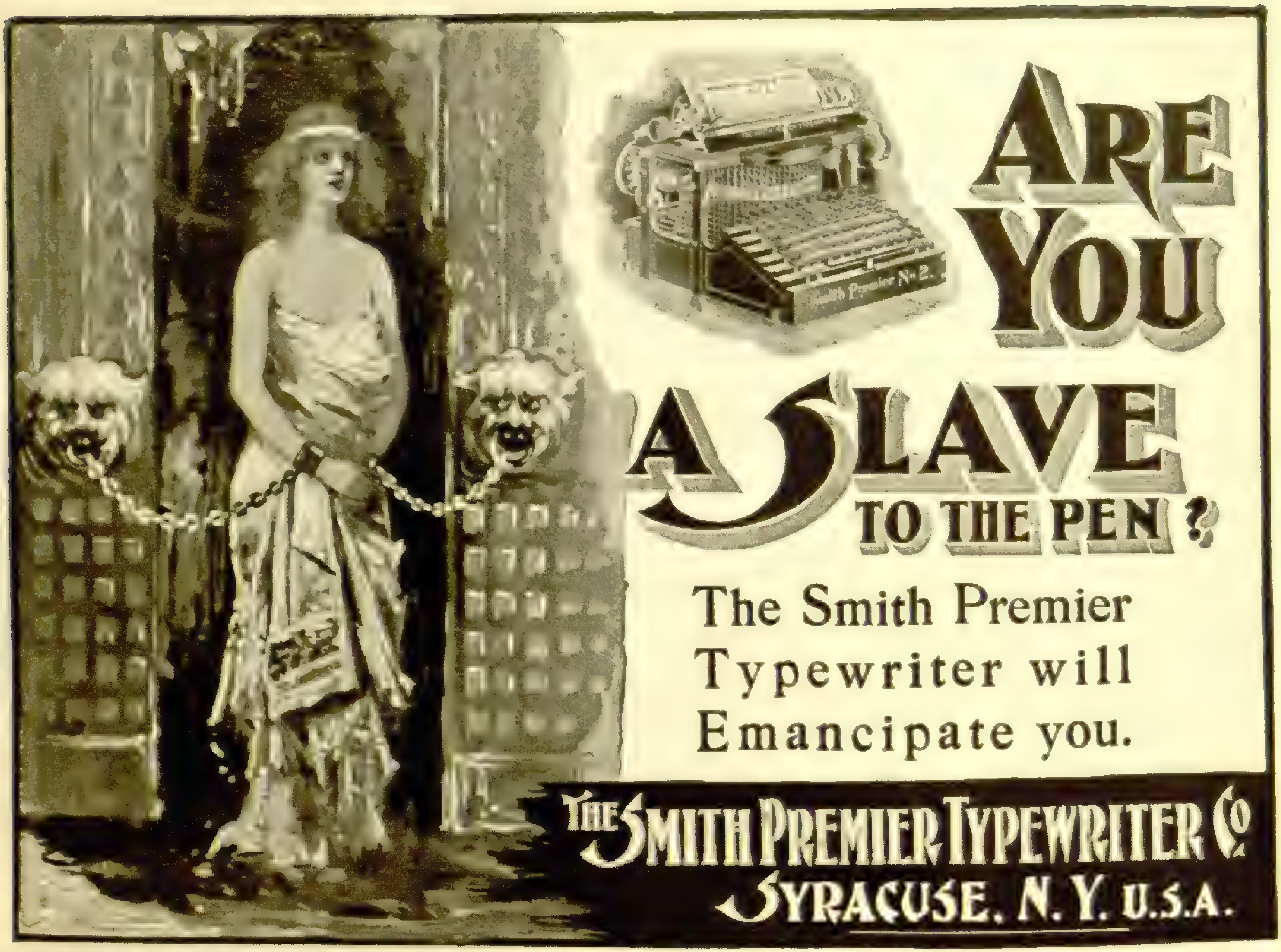

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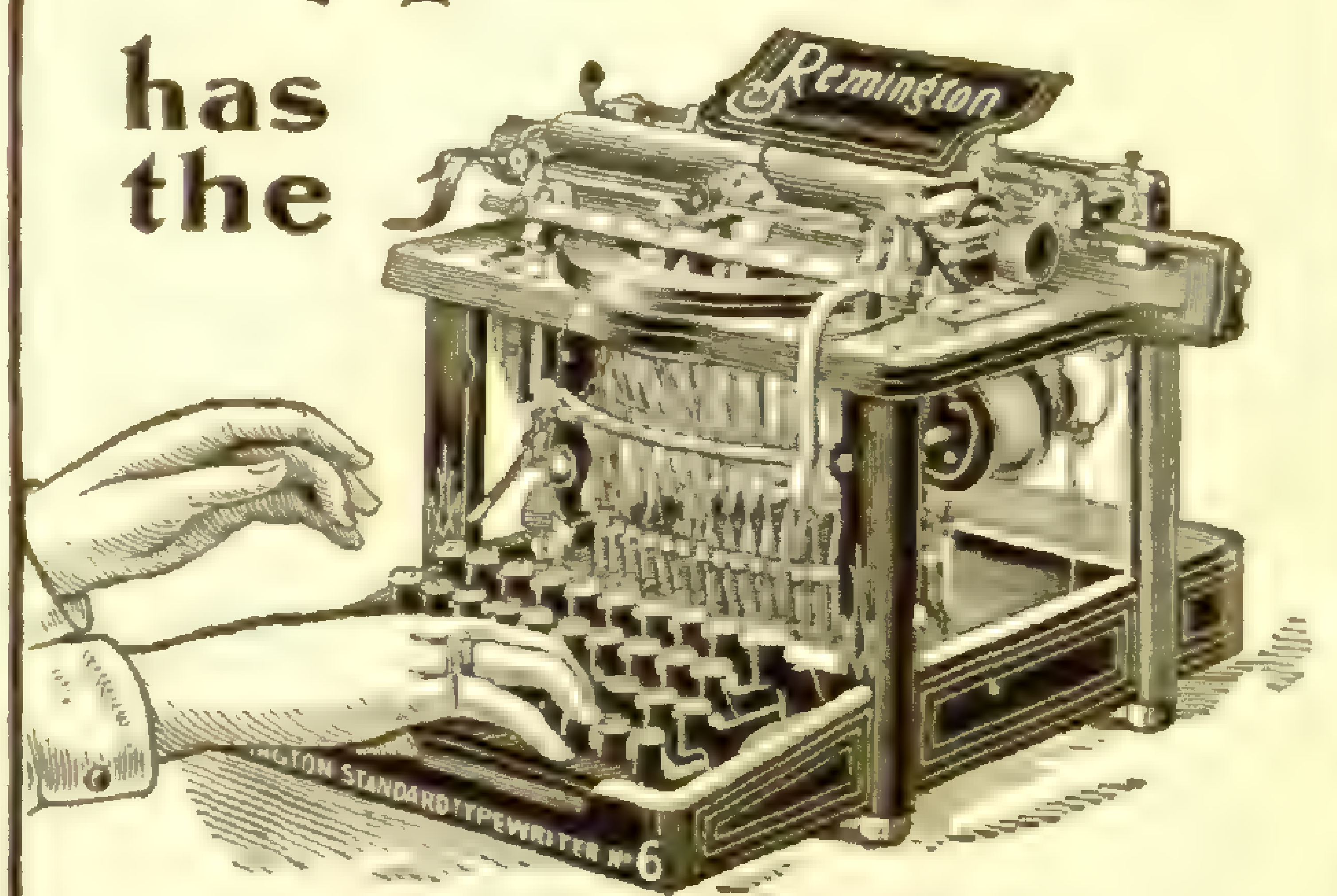
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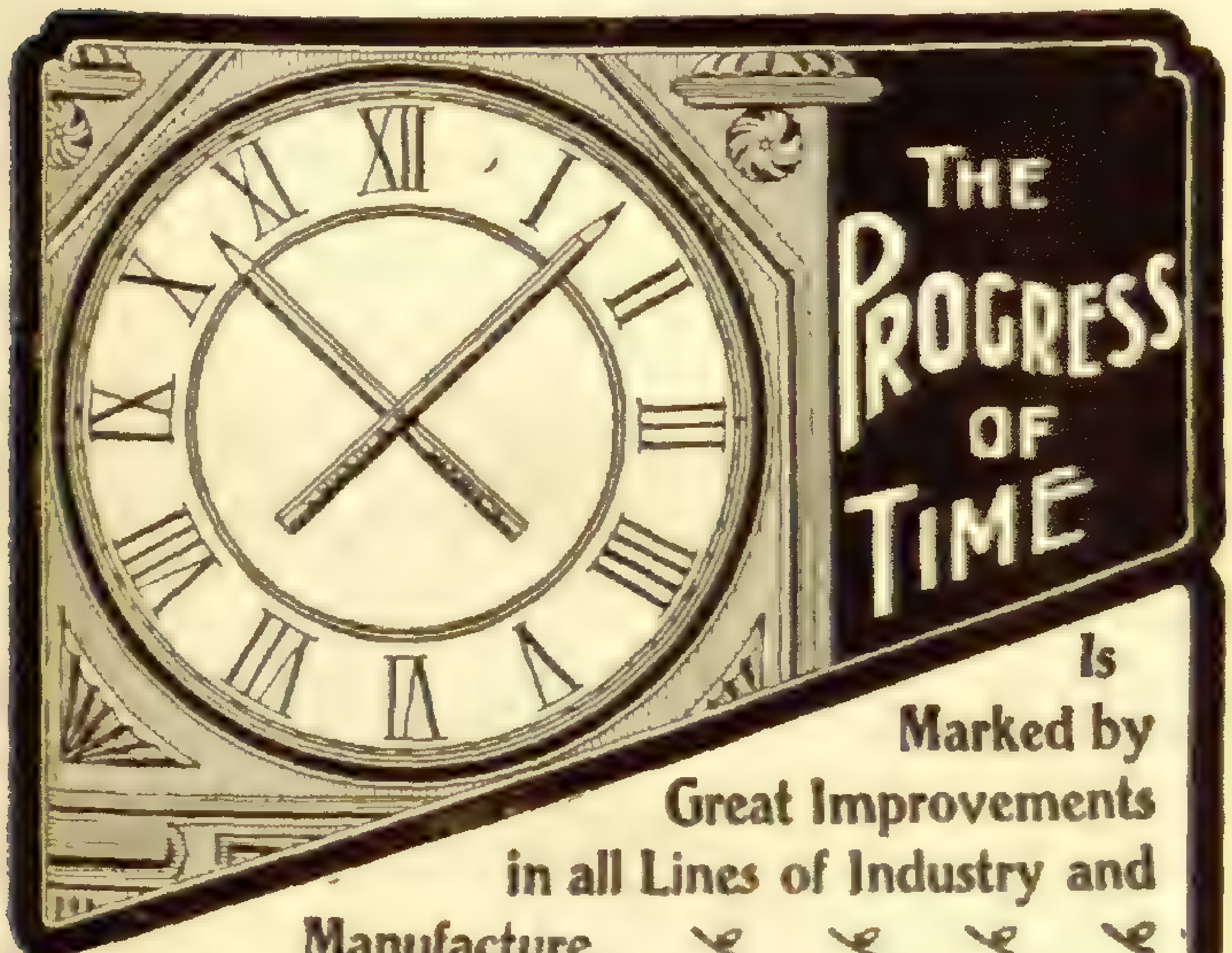
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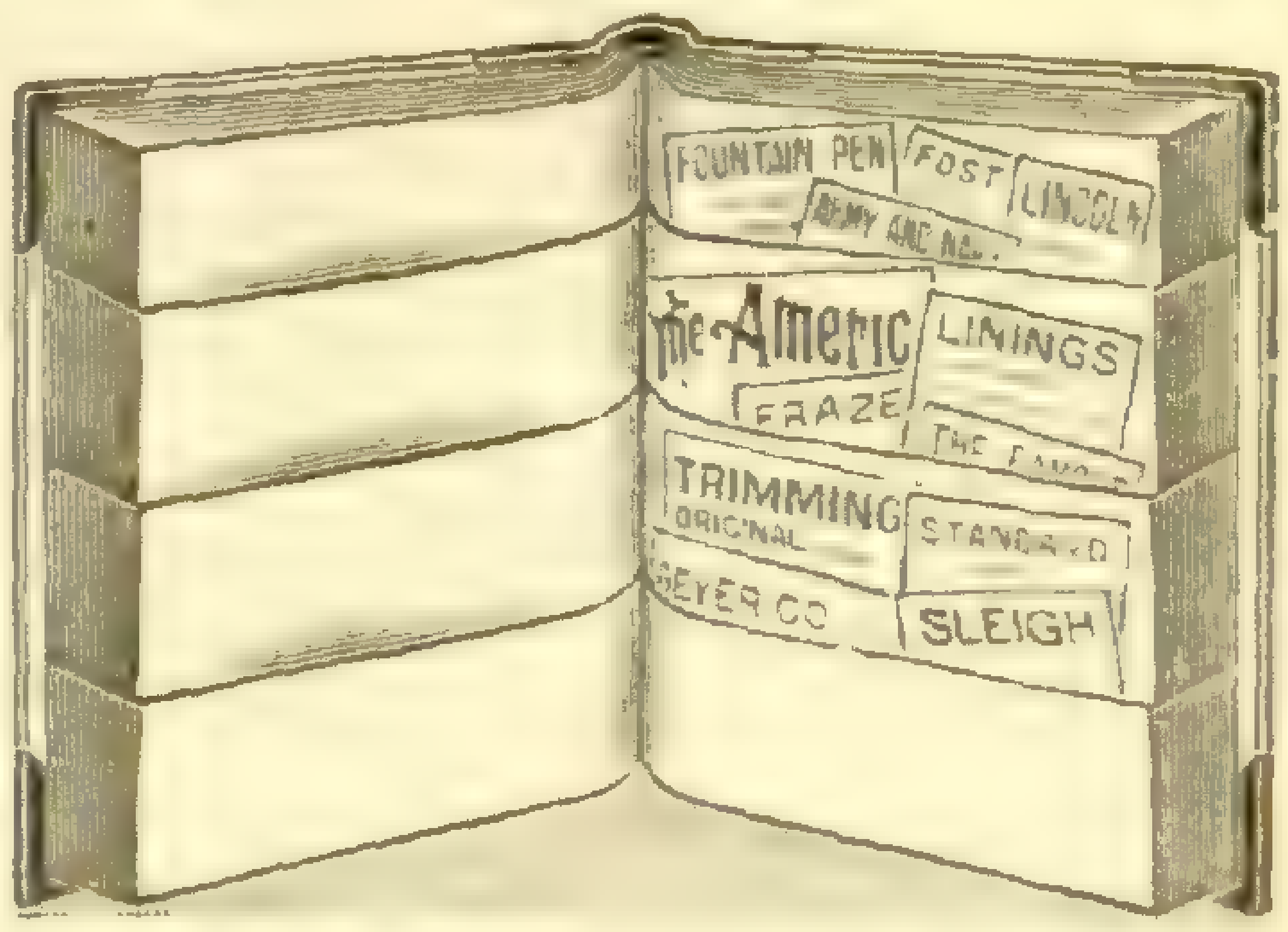
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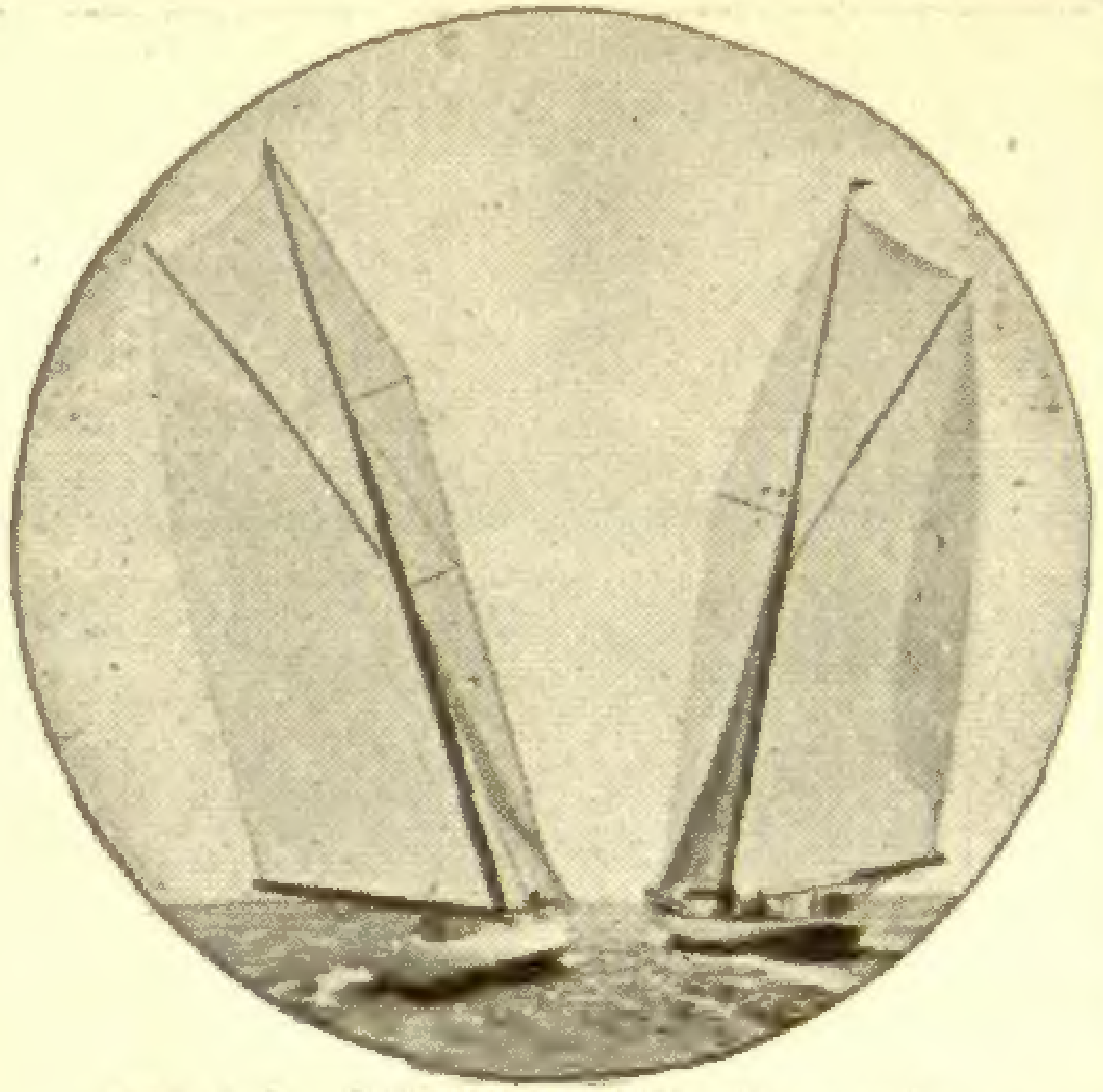

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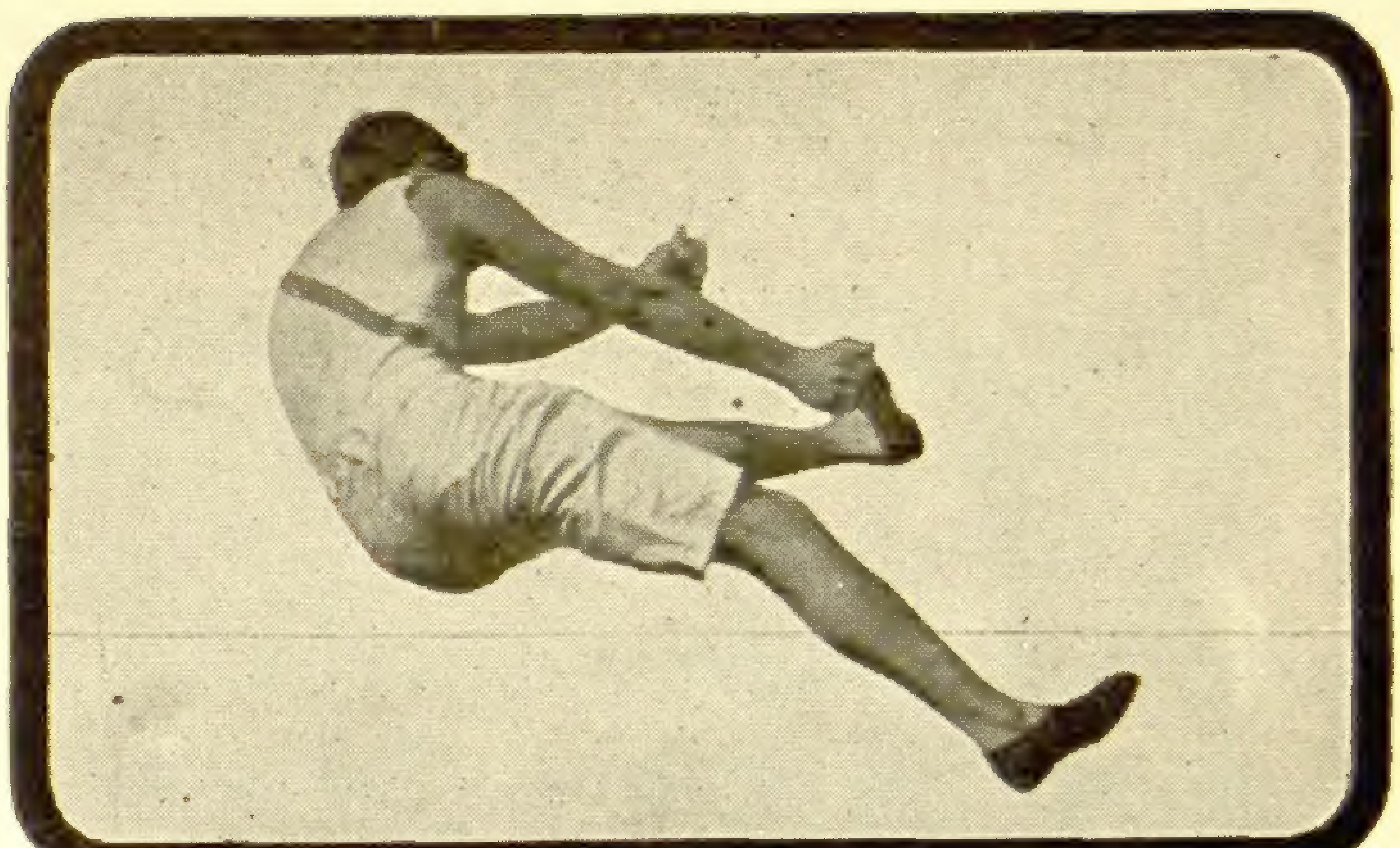

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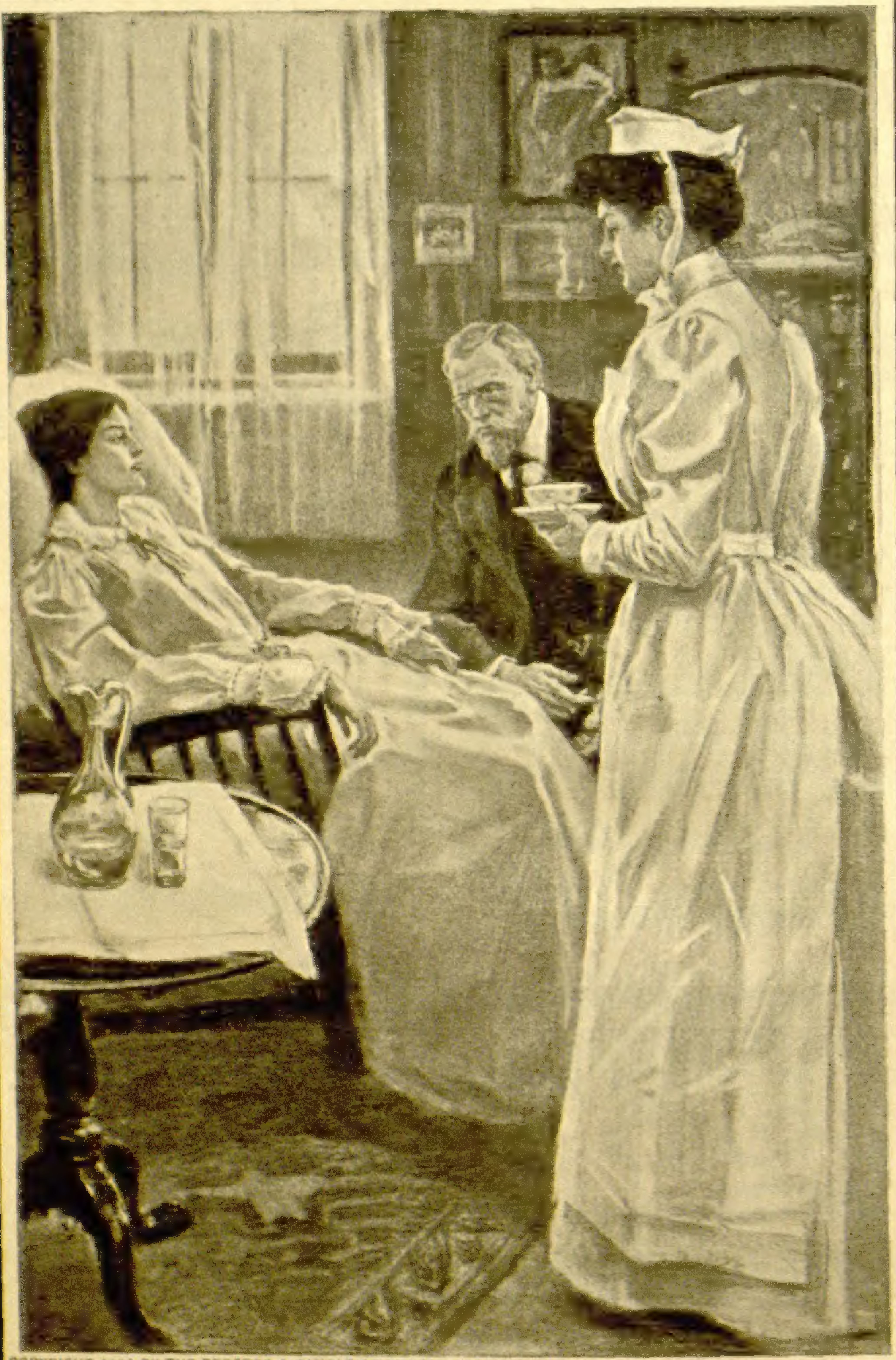

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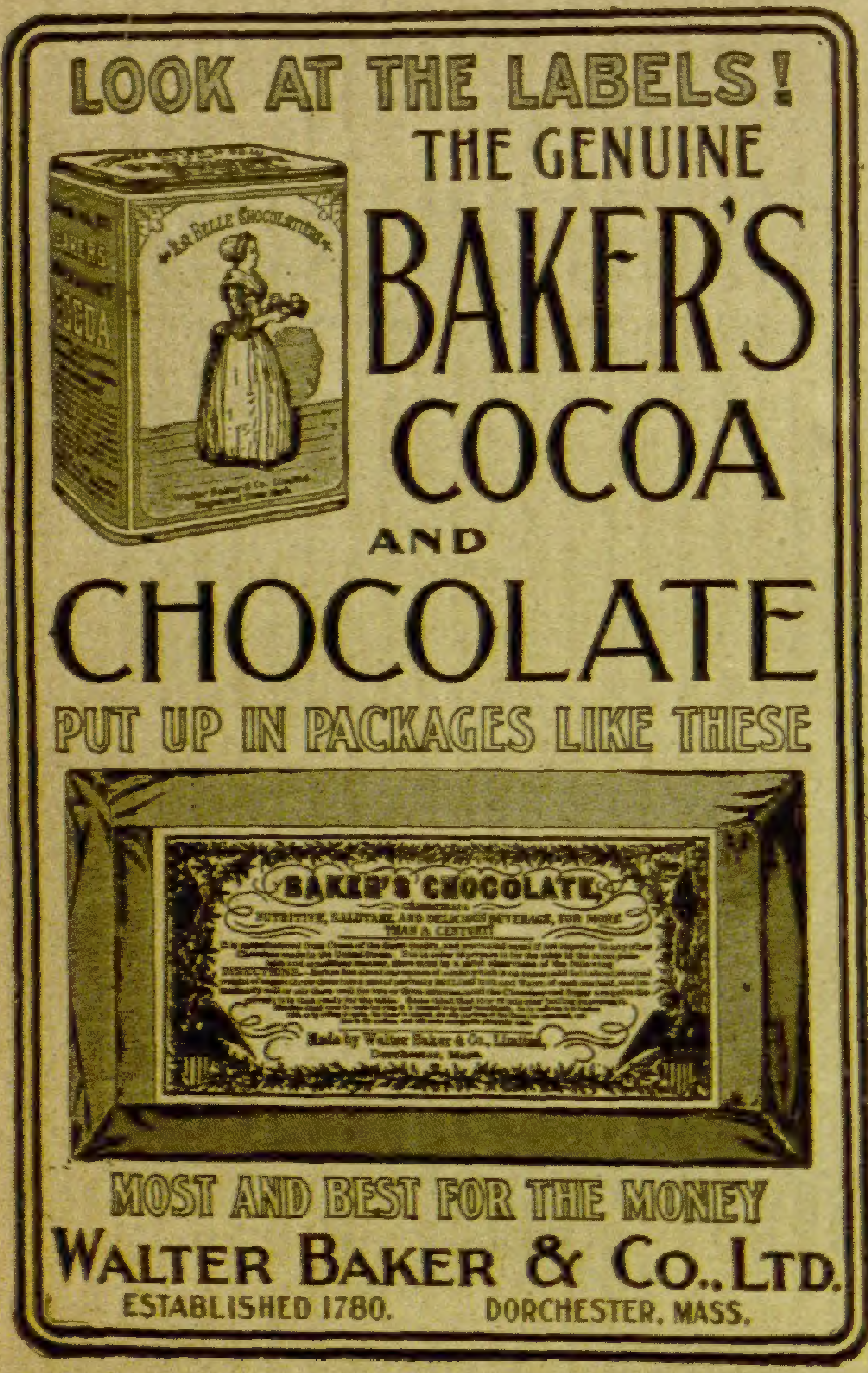

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